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Oceanic Dispersal and Behavior of Chinook Salmon in the Bering Sea

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Abstract

While Pacific salmon are widely distributed in offshore waters of the North Pacific Ocean, and of great economical and subsistence importance, little is known about their oceanic ecology. To address this knowledge gap, we tested the efficacy of pop-up satellite archival tags (PSATs) to provide insights into the oceanic movements, survivorship, behavior, and thermal environment of Chinook salmon *Oncorhynchus tshawytscha* in the Bering Sea. Tagged Chinook salmon (n = 23) were 57–89 cm fork length (68.7±9.9 cm, mean±SD) and were at liberty for 0–149 days (51.2±39.1, mean±SD). The PSATs were an effective method for gathering information about the oceanic ecology of Chinook salmon. Of the 23 tags deployed, 17 reported to satellites while six never transmitted and were considered missing. End locations of tagged Chinook salmon ranged widely between the north-central Bering Sea, the central Aleutian Islands, and the central Gulf of Alaska. While at liberty, Chinook salmon spent the majority of their time (53%) in the first 25 m of the water column (total range 0–538 m), occupying a thermal environment of 5–11°C 69% of the time. PSATs provided evidence of predation on tagged Chinook salmon by salmon sharks *Lamna ditropis* (n = 7), a marine mammal (n = 1), an ectothermic fish (n = 1), and unidentified predators (n = 2) in the Bering Sea and Gulf of Alaska. High mortality estimates in this study suggest low marine survivorship of large immature and maturing Chinook salmon. Further investigations on marine survivorship will be valuable for improving our understanding of the oceanic ecology of Chinook salmon, and may inform future management considerations by subsistence users and biological resource managers.

Introduction

While Pacific salmon are widely distributed in offshore waters of the North Pacific Ocean, and of great economical and subsistence importance, little is known about their oceanic ecology (Brodeur et al. 2000; Drenner et al. 2012; Byron and Burke 2014). This current knowledge gap stems from the fact that directed fisheries and research commonly only occur in nearshore and fresh waters. Subsequently, their offshore oceanic habits are poorly understood and based on historic high-seas fisheries, bycatch in other fisheries, and limited offshore research programs (Healy 1991; Myers et al. 1996; Myers et al. 2006; Myers et al. 2009; Sato et al. 2016). Of particular interest is the Chinook salmon *Onchorychus tshawytscha*, which has experienced declines in abundance in recent years throughout western Alaska (ADF&G 2013; Schindler et al. 2013), causing severe hardships for rural residents. While many factors (e.g., freshwater mortality, parasites) may be partially responsible, this species' decline is commonly linked to the oceanic phase of its life, about which little is known (Schindler et al. 2013). Within the oceanic phase, most recent research programs have focused on this species' first summer at-sea, resulting in a conspicuous knowledge gap in the ecology and survival of relatively large Chinook salmon that have spent at least a year in the ocean (Drenner et al. 2012).

Understanding several aspects of the oceanic phase of large Chinook salmon, including movement, vertical distribution, and thermal environment may help understand factors affecting the abundance of this species and may inform practices that alleviate unintentional mortality. Specifically, information on distribution, diel and seasonal movements, and water masses occupied can inform Individual Based Models and life history models that are used to understand population dynamics of fishes (Brodeur et al. 2000; Hinke et al. 2005a). Further, understanding the temperature preferences of Chinook salmon is valuable in understanding bioenergetics and

climate-induced changes on wild stocks (Nielsen et al. 2013). Finally, this knowledge can help answer questions concerning the susceptibility of Chinook salmon to various fishing techniques (e.g., bottom and midwater trawls), and to design spatially explicit fisheries management practices, such as time-area closures, for avoiding bycatch of this species (Smedbol and Wroblewski 2002; Hobday et al. 2010). Ultimately, new information about the oceanic habits and ecology of Chinook salmon may add to scientists' understanding of the decline in its abundance, particularly in western Alaska.

Electronic tags that record environmental variables while attached to a fish are a method to collect detailed information about the oceanic dispersal, behavior, and habitat occupancy of large immature and maturing Chinook salmon (Arnold and Dewar 2001; Thorstad et al. 2013). Previous electronic tagging efforts near California and Oregon employed a type of electronic tag called archival tags or Data Storage Tags (DSTs) that must be recovered by capturing fish. These DSTs were used to describe ocean habitat use of Chinook salmon, explore hypotheses that link population dynamics of this species to ocean temperatures, and describe patterns of behavior and habitat use in response to variable oceanographic conditions (Hinke et al. 2005a ; Hinke et al. 2005b). Additionally, DSTs have been used to investigate these questions for Chinook salmon in the Bering Sea; however, the low recovery rate of tags impeded the collection of sufficient data to infer general behavioral and dispersal patterns of this species in this region (Walker and Myers 2009).

An alternative electronic tag that may alleviate low data recovery rates for tagged Chinook salmon in the Bering Sea is the pop-up satellite archival tag (PSAT). Similar to archival tags, these tags measure and record depth, temperature and light intensity data while attached to a fish. On a preprogrammed date, this tag releases from the fish, floats to the surface of the ocean

and transmits data to satellites, which are then retrieved by project investigators. Because PSATs do not rely on recapture for data retrieval, they are a fisheries independent method of data collection. Fisheries independent technology is critically important for understanding the oceanic habits of Chinook salmon near western Alaska because there are currently no offshore directed fisheries for them or research programs in the Bering Sea. Additionally, data can be retrieved from tagged fish that experience mortality (Thorstad et al. 2013), which is likely just as important as data returned by live fish (LaCroix 2014), especially if Chinook salmon are experiencing high rates of mortality while occupying marine waters.

In the past, because of the relatively large size of the tags, the successful use of PSATs to study the movements of fishes was confined to large species such as tuna *Thunnus* spp. (Gunn and Block 2001), tiger sharks *Galeocerdo cuvier* (Holland et al. 2001), and Pacific halibut *Hippoglossus stenolepis* (Seitz et al. 2003). As the size of the tags has diminished, PSATs have been used to describe movements and habitat occupancy of smaller fishes such as the Dolly Varden char *Salvelinus malma* (Courtney et al. 2016a), Atlantic salmon *Salmo salar* (LaCroix 2013; Godfrey et al. 2015), and striped bass *Morone saxatilis* (Graves et al. 2009).

Because Chinook salmon are of similar size to other salmonid species recently studied with PSATs, we hypothesized that these tags may be a feasible method for examining the ocean phase of Chinook salmon in the Bering Sea. Therefore, the goal of this study is to evaluate the utility of using PSATs on Chinook salmon, and to provide initial insights into oceanic distribution, movements, behavior, habitat occupancy, and survivorship of Chinook salmon in the Bering Sea.

Objectives

1) Test the feasibility of using a chartered sportfishing vessel from Dutch Harbor, Alaska for capturing large, immature Chinook salmon.

2) Test the survivability of large, immature Chinook salmon that have pop-up satellite archival tags externally attached to them.

3) Provide qualitative descriptions of the oceanic habits and environment of large, immature Chinook salmon in the Bering Sea, including dispersal, large-scale distribution, and depth and temperature occupancy.

Methods

Fish capture and tagging

In mid-November to December 2013–2015, 10 Chinook salmon were captured, tagged and released near Dutch Harbor, AK in the Bering Sea (Table 1; Figure 1). During this winter sampling, fish were captured while trolling aboard the F/V *Lucille*. In addition to capturing fish near Dutch Harbor, in late July/early August 2014–2015, 13 Chinook salmon were captured, tagged, and released aboard the R/V *Hokko maru* in the central Bering Sea (Table 1; Figure 1). During this summer sampling, Chinook salmon were captured using a mid-water trawl (n=6) that contained a live box cod end and by hook-and-line (n=7).

Immediately after capture, Chinook salmon were examined and deemed appropriate for tagging if they were >60 cm fork length (FL), had no visible bleeding or large external injuries, nor were fin-clipped (indicating hatchery origin from outside of western Alaska). For tagging, Chinook salmon were carefully removed from the water of the ocean or the live box with a knotless-mesh dipnet and placed in a custom-fabricated tagging cradle (Courtney et al. 2016b) that contained flowing sea water (Figure 2). PSATs were attached to Chinook salmon using a "tag backpack" system (Figure 2), formerly used on Atlantic salmon (Chittenden et al. 2013) and

Dolly Varden (described in Courtney et al. 2016b). After a PSAT was secured to a fish, it was immediately released headfirst into the ocean. Global Positioning System coordinates at the time of release were used as a fish's tagging location. All fieldwork was conducted under University of Alaska Fairbanks Institutional Animal Care and Use Committee assurance (495247) and State of Alaska Fisheries Resource Permits (CF-13-110, CF-14-112, and CF-15-125).

Tag specifications data acquisition

All PSATs (X-tag, Microwave Telemetry, http://www.microwavetelemetry.com/fish/Xtag.cfm) weighed 40 g in air, had an overall length of 30.5 cm (maximum diameter 3.2 cm, antenna length 18.5 cm) and were slightly buoyant. While attached to a fish, the tags measured and recorded depth, temperature and ambient light intensity every two minutes. Tags released from fish, via a corrodible link, on end dates that were programmed into the tags' microprocessor, or if a tag triggered a fail-safe mechanism by remaining at a constant pressure (±2.5 m) for seven days (indicating either death and sinking to the sea floor, or detachment from the fish and floating on the ocean surface). After releasing from the fish, the tags floated to the surface of the sea and transmitted, via satellite, archived temperature and depth data, and daily sunrise and sunset times that were calculated from light intensity readings. While transmitting, the location of the tag was determined from the Doppler shift of the transmitted radio frequency in successive uplinks received during one satellite pass (Argos satellite system; Keating 1995). PSATs were programmed to collect data for 0.5–9 months, and end dates were staggered to occur during fall, winter and early spring, depending on time of tagging. As most Chinook salmon ascend rivers in early summer to spawn, this pop-up schedule was developed to ensure that the tags would pop-up while the fish were still in saltwater, as the PSAT tags need at least 5 psu saltwater for the release mechanism to function.

Because of the large amount of data collected by the tags, limited data reception by Argos satellites, and short tag-battery life while transmitting to satellites, only a subset of temperature and depth data were transmitted by the tags. In this study, the tags transmitted a subset of depth and temperature data collected every 15 minutes, except for one tag that reported data collected at the native resolution of every 2 minutes. Additionally, daily minimum and maximum depths, temperature, and light readings, extracted from the data collected every two minutes, were transmitted. It is important to note that some individual temperature and depth readings reported by the tag may be slightly less or greater than the true values that the tag sampled (Brunnschweller 2014). These inaccuracies, termed "delta limited" data, result from the tags' data sampling, compression, and reporting algorithms (http://www.microwavetelemetry.com/fish/understanding_data_xtag.cfm). However, delta limited values made up a small percentage of the depth and temperature records (<0.001% of the total data set), therefore, they were retained in the datasets and used for data analyses (e.g., Howey-Jordan et al. 2013). Transmitted daily sunrise and sunset times were used to calculate daily latitude and longitude estimates using the tag manufacturer's proprietary software during post-processing of transmitted data. For tagged Chinook salmon that were alive on their scheduled end dates (i.e., programmed release dates), end locations of tagged fish were considered as the first transmission with an Argos location class ≥1, which translates into a position error of <1.5 km. For tags that released because of activation of the fail-safe constant-pressure release mechanism (resulting from mortality when depth was >0 m or premature tag detachment and subsequent floating on the surface when depth=0), end dates were considered the date of predation, mortality, or premature tag detachment. In these cases, each tag's end location was reconstructed by subtracting the estimated drift vector (direction and distance) traveled by

the tag while floating on the surface of the ocean between initially floating to the surface of the ocean and reporting to satellites (e.g., Chittenden et al. 2013). Drift vectors of tags were approximated by calculating the mean distance and direction of a drifting tag travelled during the first 24 hrs after reporting to satellites, and extrapolating to the entire period of drifting by multiplying the one-day vector by the days of drift.

Data analyses

Efficacy of tags for studying Chinook salmon

To evaluate the utility of using PSATs to study Chinook salmon, two main metrics were examined, tag reporting rate and percentage of data retrieved. Tag reporting rate was determined by tabulating the percentage of tags for which end locations could be determined. Percentage of retrieved depth and temperature data were calculated as the total number of individual depth and temperature readings received via Argos satellite system, divided by the hypothetical amount of data that should have been transmitted and received by satellites.

Spatial distribution and movement

Distribution and movement of Chinook salmon in the Bering Sea were described by examining net movement and at-liberty distribution. First, net movement between tagging and end dates was examined by mapping tagging and end locations in GIS software (ArcMap 10.1; Environmental Systems Research Institute Inc., Redlands, California). End locations were aggregated by geographic region s (i.e., central Bering Sea, eastern Bering Sea/Aleutian Islands, Gulf of Alaska). Minimum dispersal distance was determined by calculating the great arc circle distance of a non-meandering route that did not pass over land between tagging and end locations. Second, distribution of tagged Chinook salmon while at-liberty, i.e., between tagging

and end dates, was examined. To accomplish this, we attempted to reconstruct individual fish movement tracks by analyzing daily geolocation estimates with state-space movement models (i.e., KFTrack [Seibert et al. 2003] and UKFFST [Lam et al. 2008]). Prior to modeling movement, daily geolocation estimates were filtered because of relatively large errors associated with light-based geolocation (Arnold and Dewar 2001), especially around the spring and fall equinoxes (Chittenden et al. 2013). The filtering process consisted of discarding daily geolocation estimates 10 days before and after the equinoxes and those that were on land (i.e, not plausible; Chittenden et al. 2013). Additionally, because light attenuation at depth can cause large errors in calculating daily sunrise and sunset events, all daily geolocation estimates that resulted from periods when the tagged fish were >10 m deep were discarded. This filtering process removed most unrealistic and likely erroneous daily geolocation estimates (Figure 3). However, even after the filtering process, the state space models failed to converge and produce individual movement tracks.

Considering this, we used a broader scale approach, a home range analysis, to understand distribution while at-liberty. In this analysis, filtered daily geolocation estimates of all tagged fish were mapped in GIS software, and 50%, 75%, and 90% utilization distributions were calculated using the 'home range tool package'(Rodgers et al. 2015) in ArcMap 10.1. In addition to home range analyses, to ascertain when fish likely moved from one hydrographic region to another (e.g., eastern Bering Sea to Gulf of Alaska), tag-recorded depth- temperature profiles were qualitatively compared to published seasonal trends in the oceanographic properties of the Bering Sea and Gulf of Alaska (Stabeno et al. 1999; Stabeno et al. 2001).

Depth and temperature occupancy

To describe depth and temperature occupancy of tagged fish, several metrics were calculated. First, for each tag's entire time at liberty, minimum, maximum, and mean (±SD) occupied depths and temperatures were calculated. Grand mean (±SD) depths and temperatures were also calculated by aggregating records from all tags. Second, overall and monthly mean (±SD) proportion of time that all Chinook salmon spent at depth (25 m bins) and temperature (1°C bins) intervals was calculated.

To examine potential diel differences in the depth and temperature occupancy of Chinook salmon, diel periods (i.e., night and day) were determined from sunrise and sunset events near Dutch Harbor, AK (http://aa.usno.navy.mil/data/docs/RS_OneDay.php). To avoid crepuscular behaviors that may not be representative of typical diel behaviors, periods of twilight (i.e., sun is 0–18° below earth's horizon) were omitted from analyses. After defining diel periods, individual time series of depth and temperature were visually examined for diel differences. To examine overall differences in diel depth and temperature occupancy of tagged fish, mean daily depths and temperature, for diel periods (i.e, day and night) were calculated for all tag data combined (i.e., pooled). A Wilcoxon sum rank test was used to detect significant differences (α=0.05) between diel periods in mean ranks of daily mean depths and temperatures. Subsequently, diel differences in daily mean depth and temperatures were examined on a monthly basis (α=0.05).

Mortality

In this study, mortality of tagged fish was identified by qualitatively examining light, depth and temperature data. Previous PSAT research has identified several types of mortality, including predation by ectothermic and endothermic fish, as well as marine mammals (e.g.,

Béguer-Pon et al. 2012; Lacroix 2014; Consgrove et al. 2015). In this study, predation mortality was qualitatively identified by one or a combination of the following tag data: a rapid change in ambient temperature indicating consumption by an endotherm; complete darkness for >24 hrs indicating that the tag was in the stomach of a predator; and/or abrupt changes in depth-based behavior indicating depths occupied by a predator were different than those occupied by the free-swimming Chinook salmon prior to predation. Identification of likely predators was inferred from known visceral temperatures, distribution, and depth-based behavior of potential marine predators in the North Pacific Ocean.

Mortality due to capture/tagging effects or unconfirmed predation were inferred when tag data suggested that tagged fish sank to the sea floor and remained at a constant depth, until the 7-day constant-depth release activated and the tag floated to the surface and transmitted to satellites. If mortality occurred within one week of tagging, and depth and temperature records indicated abnormal behavior, these events were considered to be capture/tagging induced mortality. If depth and temperature records had durations >1 week and a fish's behavior prior to death appeared similar to behavior of other tagged Chinook salmon, it was considered to be unconfirmed predation event. In this scenario, it was inferred that the tagged fish was torn into pieces by a predator and the portion of the carcass with the tag sank to the sea floor (LaCroix 2014).

Similar to tagged Chinook salmon, depth and temperature occupancy of inferred predators of tagged Chinook salmon were described. For each predator, individual minimum, maximum and mean (±SD) depth and visceral temperatures were calculated. To obtain the most accurate internal temperatures of predators, only temperature readings taken after stomach temperatures became stable were used in data analyses (Goldman et al. 2004). Additionally, the

proportion of time spent at discrete depth (25 m bins) intervals was calculated for each predator. To understand the predators' internal temperature in relation to ambient water temperatures, the thermal excess (T_e) was calculated as the difference between mean stomach temperature (T_s) and mean ambient temperature immediately before predation (T_{a1}) and after tag expulsion (T_{a2}) (LaCroix 2014; Consgrove et al. 2015).

To understand the possible trends of capture/tagging on Chinook salmon behavior and survivorship, mean size (FL) among fish whose tags were ingested by endothermic predator, experienced mortality (predation + unidentified predation + capture/tag-induced mortality), and those that were alive on their end dates were examined through descriptive statistics, including means and 95% confidence intervals.

Evaluation of project objectives

In addition to the qualitative and statistical analyses, each study objective was evaluated using semi-quantitative metrics described in the original research proposal for this project.

Objective 1: Success will be defined as capturing and tagging ≥1 large, immature Chinook salmon per day.

Objective 2: Success will be defined as survivability of ≥50% of the tagged fish

Objective 3: Success will be defined as recovering light, depth and temperature data from ≥50% of the tagged fish

Results

Tagged Chinook salmon were 57–89 cm fork length (68.7±9.9 cm, mean ±SD) and were at liberty 0–149 days (40±42 d, mean±SD; Table 1). Of the 23 tags deployed, 17 (74% of the total 23) reported to satellites and six (26% of the total 23) never transmitted and were considered missing (Table 1). Of the 17 tags that transmitted to satellites, three reported on the

programmed end date and the remaining 14 tags reported early due to activation of the fail-safe constant-pressure release mechanism. The percentage of data received by Argos satellites varied between 5 and 100% (80.9±26.5%, mean±SD; Table 1; Figure 4). The number of data sets available for analyses varied seasonally, with most data recorded during August–January and none from May to July (Figure 5).

Spatial distribution

End locations of tagged Chinook salmon were in the central Bering Sea (n = 5), eastern Bering Sea/Aleutian Islands (n = 10), and western and central the Gulf of Alaska (n = 2; Figure 6). Of the tags deployed in the central Bering Sea during August, end locations (Figure 7), utilization distributions (Figure 8), and depth-temperature profiles suggested that most remained in the vicinity of the region while at liberty for 14–149 days. However, one fish (#133395) that was at liberty for 78 days dispersed in a southeastern direction and reported over 540 km away from the tagging location in the eastern Bering sea (Figure 7). For Chinook salmon tagged during the winter near Dutch Harbor, end locations (Figure 7), utilization distribution (Figure 8), and depth-temperature profiles suggested that most remained in the southeastern Bering Sea from Dutch Harbor, AK to the outskirts of Bristol Bay. In contrast, one fish (#142198) dispersed in a southwesterly direction to just south of the central Aleutian Islands by January (Figure 7). Additionally, two tagged fish (#129843 and #142199) reported from the Gulf of Alaska, 815 and 1470 km away from their tagging locations (Figure 7). Based on depth and temperature profiles, these two fish exited the Bering Sea in early January.

Depth and temperature occupancy

While at liberty, Chinook salmon occupied depths ranging from 0 to 538 m (50.2±61.3 m; grand mean±SD) and experienced a thermal environment ranging from -0.55 to 13.53°C (Table 2). When all tag records were aggregated, Chinook Salmon spent the majority (53%) of their time in the first 25 m of the water column (Figure 9) occupying a thermal environment of mostly 5–11°C (69% time at-liberty). In general, Chinook salmon occupied their shallowest warmest water in August–October, and the deepest coolest waters in January–March (Figure 10). Overall, tagged Chinook salmon spent significantly ($p < 0.05$) more time in shallower, warmer waters at night, and deeper, cooler waters during the day. When examined on a monthly basis, significant differences ($p < 0.05$) in mean diel depths existed during winter (January–March) and fall (September–October), but not during spring and summer (Figure 10). For example, one fish (#129843) that was tagged near Dutch Harbor in December demonstrated diel depth occupancy in February and early March, but not in late March and April (Figure 11). Additionally, another tagged Chinook salmon (#142189) that was tagged in the central Bering Sea in August demonstrated diel differences in depth and temperature occupancy in September–October, but not in the months of November–December (Figure 12). Similar to diel differences in depth, significant differences ($p < 0.05$) in mean temperatures between diel periods were found in winter (February–March) and fall (August–October) months (Figure 13). As a complement to these overall trends in diel behaviors, qualitative visual analyses of depth and temperature records revealed some individual variation in diel behaviors. For example, while not common, some fish did demonstrate periodic diel behaviors during the months of August, November, and December that contrast to the trends identified when all data records were aggregated.

Mortality

Confirmed and unconfirmed predation of Chinook salmon was relatively common in the central and eastern Bering Sea, near the Aleutian Islands, and in the Gulf of Alaska (Figure 14). Comparison of lengths between tagged Chinook salmon that had been eaten (range 59–89 cm; Table 2) or were alive on their pop-up date revealed little observable differences in size, as means and 95% confidence intervals of the two groups overlapped (Figure 15).

Based on known visceral temperatures and species distribution (Anderson and Goldman 2001; Goldman et al. 2004; Goldman and Musick 2008), seven confirmed predation events were attributed to salmon sharks *Lamna ditropis* (Table 3; Figure 15). This inference was based on temperature readings rapidly increasing from ambient water temperatures of 5–10°C to 20–26°C and the most likely place in the Bering Sea where the ambient temperature is consistently 20–26°C is in the stomach of a salmon shark (Anderson and Goldman 2001; Goldman et al. 2004). While PSATs were in the stomach of salmon sharks for 1.15–5.49 days, maximum and mean visceral temperatures of individuals ranged between 24.6–26.7°C and 21.6–25.2°C respectively (Table 3). Thermal excess (T_e) of individual salmon sharks ranged from 13.4–19.2°C (Table 3). The depth range of salmon sharks was 0–328 m (54.2±79.9 m, grand mean ±SD). In general, most sharks occupied relatively deep water while demonstrating oscillatory diving behavior during the day, and shallow water occupancy and little diving behavior at night (Figures 16 and 17). In contrast, one salmon shark remained in the first five meters of the water column while the PSAT was in its stomach for 1.15 days (Table 3).

In addition to salmon shark predation, one confirmed predation event was attributed to a marine mammal. This inference was based on temperature readings rapidly increasing from ambient water temperatures of 4–5°C to 37–38°C (Gales and Renouf 1993, Austin et al. 2006,

Kuhn and Costa 2006). While the tag was in the stomach of this marine mammal for 1.84 days, the mean temperature was 37.4±0.4°C and the thermal excess (T_e) was 32.4ºC (Table 3; Figure 18). Dives to 10 meters were common during the first six hours, after which the predator remained mostly at a depth of 0 m, indicating occupation of shallow water or possibly land (Table 3; Figure 18).

Another confirmed predation event provided evidence of ingestion by an ectothermic fish. Unlike other confirmed predation events, no observable differences in ambient temperatures were found before and after consumption of the tagged Chinook salmon. However, an abrupt change in depth occupation was evident in the data that coincided with the tag's light sensor indicating complete darkness for several days (Figure 19). While in the stomach of this predator for approximately six days, the mean temperature was 6.0±0.4°C (Table 3; Figure 19), and occupied depths were 0–274 m (125±55 m, mean±SD).

In addition to confirmed predation events, two fish experienced capture/tagging-induced mortality within 24 hrs of release, and two experienced unconfirmed predation events 7–30 days after release (Figure 20). Furthermore, one tag released from a Chinook salmon before its programmed end date with no indication of predation, and was considered to be a premature tag detachment.

Evaluation of project objectives

Objective 1: Success will be defined as capturing and tagging ≥1 large, immature Chinook salmon per day.

Fishing from a sport fishing vessel in Dutch Harbor, AK during the winter, yielded 0.4 tagged fish·day^{-1} (Table 4), therefore not meeting the criterion for successfully achieving objective 1.

Objective 2: Success will be defined as survivability of ≥50% of the tagged fish

Only two Chinook salmon in this study appeared to die from capture/tagging induced effects, providing a survivorship estimate of 91% for tagged Chinook salmon; therefore, meeting the criterion for successfully achieving objective 2.

Objective 3: Success will be defined as recovering light, depth and temperature data from ≥50% of the tagged fish

Overall, the reporting rate of tags was 75% (17 of the total 23): therefore, meeting the criterion for successfully achieving objective 3 (>50% of all tagged fish).

Discussion

PSATs in this study had high reporting and data recovery rates, and provided detailed temperature and depth records of Chinook salmon in the Bering Sea, near the Aleutian Islands, and Gulf of Alaska. Thus, results from this study provided a preliminary glimpse of the oceanic ecology of this fish species, including natural mortality caused by sharks, marine mammals, and ectothermic fish. While information collected in this study is qualitative, it highlights the efficacy of PSATs for studying Chinook salmon, and provides information from which future hypotheses can be developed.

Spatial distribution

Although clear patterns in spatial distribution were not evident because the sample size of tagged fish in this study was small, the majority of Chinook salmon remained in the Bering Sea or near the Aleutian Islands, with a smaller component moving to the central Gulf of Alaska. Even though the utilization distributions suggested two core areas of occupation in the central Bering Sea and the southeastern Bering Sea/Aleutian Island, it is likely that this result is an artifact of tagging/fishing in these two areas and short deployments of tagged fish due to predation (i.e., short times at liberty). Therefore, they likely do not represent the overall spatial distribution of Chinook salmon in the Bering Sea, which would require a larger sample size of tags and longer tag deployments to discern.

The variation in movement distances and directions of individual tagged fish between tagging and end locations is likely explained by an interaction between the time of year of tagging and the stock-of-origin of each fish. Currently, it is thought that immature Chinook salmon from many areas, including Russia, Alaska, British Columbia, and the Pacific Northwest commonly use the Bering Sea as a summer foraging area. After feeding in the highly productive Bering Sea, Chinook salmon from central Alaska to the Pacific Northwest then make southerly movements to overwinter in the North Pacific Ocean south of the Aleutian Islands or the Gulf of Alaska (Healy 1991; Myers et al. 2006; Myers et al. 2009; Larson et al. 2013). In contrast to these populations, Chinook salmon from western Alaska are thought to reside in the Bering Sea year-round (Myers et al. 2006; Davis et al. 2009; Larson et al. 2013). While there, these western Alaskan fish are thought to summer in the central Bering Sea shelf and basin, and winter over the eastern Bering Sea shelf (Larson et al. 2013). Given the differences in movement patterns among fish from different stocks and that we likely tagged fish from several stocks (Healy 1991; Myers

et al. 2006; Larson et al. 2013), it is probable that any tagged Chinook salmon in this study that left the Bering Sea during winter was likely natal to a river outside of western Alaska. Specifically, the two fish whose tags reported from the central Gulf of Alaska were likely swimming back to their natal rivers in British Columbia or the Pacific Northwest, based on their size and direction of travel. The corollary that fish that remained in the Bering Sea were from western Alaska is not necessarily true, as many of the tags were attached to these fish for short durations during the summer. As such, these tag deployments did not coincide with times that Chinook salmon were likely to move from the Bering Sea to the Gulf of Alaska, and therefore it is difficult to speculate on their natal rivers.

Depth and temperature occupancy

Depth and temperature information from tagged Chinook salmon demonstrate the ability of this species to occupy a variety of depths and thermal environments, and provides evidence of pronounced seasonal shifts in behavior. In general, tagged fish in this study showed seasonal behaviors of shallow water occupancy during the summer when occupying the central Bering Sea basin and slope followed by a transition to deeper cooler waters while occupying the eastern Bering Sea shelf during winter. These results corroborate similar insights from past research on three archival tagged Chinook salmon (Walker and Myers 2009; Walker unpublished data).

While our observations are similar to previously research in the Bering Sea, these collective observations are in direct contrast to of the behavior of Chinook salmon off the coast of Oregon and northern California. In this southern region, Chinook salmon almost exclusively occupied a narrow range of water temperatures (8–12°C) during all seasons of the year and regardless of the tagging location (Hinke et al. 2005b). To occupy this narrow range of temperatures, Chinook salmon actively adjusted their vertical position in the water column (0–

300 m). In contrast, PSATs provided evidence that Chinook salmon do not occupy a narrow range of preferred temperatures in the Bering Sea, similar to results from a previous archival tagging study (Walker and Myers 2009). Therefore, it is likely that the thermal environment experienced by the fish in the Bering Sea is more closely related to seasonal changes in water temperature and distribution of prey than active thermoregulation by changing depth.

In general, diel patterns in depth and temperature occupancy, in which Chinook salmon occupied deeper cooler waters during the day and shallower warmer waters at night, were most observable during September–October and January–March. This diel diving behavior, and its discontinuous occurrence, is similar to that of other salmonids in the central Bering Sea (Walker and Meyers 2009). Additionally, archival tags deployed on Chinook salmon in Southeast Alaska have demonstrated several different patterns in depth-specific behaviors, including some similar to those in this study (Murphy and Heard 2001; Murphy and Heard 2002). In contrast, other Chinook salmon tagged near Southeast Alaska demonstrated behaviors in which they occupied deeper waters at night and shallower waters during the day (Murphy and Heard 2001; Murphy and Heard 2002). Furthermore, research on Chinook salmon off the coast of Oregon and California during the fall found no observable patterns in depth-specific behavior by Chinook salmon (Hinke et al. 2005a), suggesting that the presence of this behavior is likely influenced by season and geographic location. While the reasons for diel behaviors is poorly understood, it is likely affected by a combination of factors including foraging, thermoregulation, and/or predator avoidance.

Mortality

Perhaps the most intriguing result of this study is the high proportion of tags that provided evidence of predation by endothermic, ectothermic, and unidentified predators.

Furthermore, this study provides evidence that salmon shark predation may be a substantial source of oceanic mortality of immature and maturing Chinook salmon. Predation by salmon sharks occurred during both the summer and winter, and throughout a wide range including the central and eastern Bering Sea, and near the Aleutian Islands. Even if PSATs increased the vulnerability of Chinook salmon to predation, these findings indicate that salmon sharks may be spatially and temporally widespread and co-occur with Chinook salmon during all periods of the year. The potentially frequent incidence of salmon shark predation on Chinook salmon is corroborated by a previous estimate that salmon sharks have the capacity to consume a considerable proportion of salmon (*Oncorhynchus* spp.) residing in the Bering Sea and Gulf of Alaska on an annual basis (Nagasawa 1998).

Unlike predation by salmon sharks, which have unique internal temperatures, the culprits of the marine mammal and ectothermic predation events is much more speculative. In the case of marine mammal predation, based on its affinity for surface waters and possibly land, we speculate that the predator was a pinniped such as a Stellar sea lion *Eumetopias jubatus*, which frequently occur in the area of the predation event. In the case of predation by an ectothermic fish, based on the locality of predation and depth-based behaviors of the predator, we speculate that predation was likely from a large fish, such as a Pacific halibut (Seitz et al. 2011), or sleeper shark *Somniosus pacificus* (Hulbert et al. 2006).

Understanding the potential impact of low oceanic survival of large immature and maturing Chinook salmon is important, as there is a long standing assumption that the ocean is relatively safe once salmon have survived the critical periods of ocean entry and first ocean winter (Beamish and Mahnken 2001). Recently, declines in both size and age of maturity of Chinook salmon have been documented throughout western Alaska (Lewis et al. 2015). While

evidence of size-selective harvest may be driving early maturation in Chinook salmon, researchers have hypothesized that additional factors including environmental conditions in the ocean and density dependent effects may be responsible for the decline of older age classes of Chinook salmon returning spawning grounds (Lewis et al. 2015). We hypothesize that large apex predators, such as salmon sharks, large ectothermic fish and marine mammals, offer another potential factor contributing to the decline of older age classes .Similarly, predation by porbeagle sharks *Lamna nasus* and Atlantic bluefin tuna *Thunnus thynnus* on the large oceanic life stage of imperiled Atlantic salmon *Salmo salar* has been hypothesized as an important factor hindering the recovery of stocks from Canadian rivers (Lacroix 2014). Future studies are needed to advance the collective knowledge about oceanic mortality of Chinook salmon and provide a more holistic description of their ocean (Okey et al. 2007).

While salmon shark biology was not a study objective, PSATs collected valuable information on the visceral temperatures and vertical distribution of salmon sharks occupying the Bering Sea and nearshore waters of the Aleutian Islands, about which little is known (Goldman and Musick 2008). The visceral temperatures of salmon sharks in this study were similar to those of previous studies (Anderson and Goldman 2001; Goldman et al. 2004), and demonstrated the amazing ability of salmon sharks to maintain stable, elevated internal temperatures 15–20°C above ambient water temperatures. Elevation of internal temperatures is thought to increase this species' ability to make rapid dives through stratified water (150–300 m in this study), maintain high sustained swimming speeds, and occupy relatively cold temperate and subarctic habitats (Weng et al. 2005; Goldman and Musick 2008; Weng et al. 2008, Watanabe et al. 2015). These capabilities allow salmon sharks to be apex predators throughout their range in the North Pacific Ocean, including the Bering Sea.

Interestingly, there was evidence that salmon sharks occupy the Bering Sea during the winter, where ambient water temperatures were 4–5ºC. While Salmon sharks previously have been found to occupy subarctic environments of the North Pacific Ocean, including the Bering Sea, most research suggests that they make southerly movements out of these cold habitats by the onset of winter (Weng et al. 2005; Weng et al. 2008; Goldman and Musick 2008). In contrast, results from this study suggest that not all Salmon sharks leave the Bering Sea during the wintertime. With the current warming of the Bering Sea (Stabeno et al. 2007) and known endothermy of salmon sharks (Goldman et al. 2004), future research is important to understand the possible expanding niche of salmon sharks (Weng et al. 2005), and the role of salmon sharks in mortality of Pacific salmon (Okey et al. 2007). The importance of understanding these apex predators in the Bering Sea ecosystem cannot be understated.

The frequency of unconfirmed mortality events suggests that the six missing tags and one tag that prematurely detached from a fish also may have been preyed upon. Each tag was programmed with an emergency release mechanism that is triggered by exceeding a water depth of 1250 m, to ensure that a tag is not crushed by excessive pressure (>2500 m). As a result, missing tags are likely not a result of capture/tagging mortality of fish that sink to the seafloor in deep areas such as the Bering Sea basin. We speculate, admittedly with no evidence, that the missing tags are the result of being destroyed while tagged Chinook were consumed by predators. In the case of the one tag that prematurely detached from the fish and floated on the surface of the ocean, the tag may have been ripped free from the salmon during a predation event, which has been previously inferred from other similar research on Atlantic salmon (LaCroix 2014). If assigning these events to natural mortality by predation, survivorship of tagged Chinook salmon by predation in this study drastically decreased from 52% (11 out of 23)

to 22% (18 out of 23). However, the subjectivity of assigning mortality events makes it impossible to understand the actual oceanic mortality of tagged Chinook salmon.

PSAT evaluation

PSATs have provided unprecedented insight into the distribution, behavior and thermal environment of Chinook salmon, information that were previously difficult to collect. PSATs in this study had a reporting rate of 75%, which is vastly higher than past electronic tagging studies in the Bering Sea that suffered from low recovery rates (e.g., Walker et al. 2005). This difference in tag recovery rates highlights the utility of PSATs for studying Chinook salmon.

While tag reporting and data recovery rates were relatively high in this study, fine-scale fish movement paths were not able to be produced with post-hoc state space models. This is in part because the models rely on relatively accurate daily geolocation estimates. In this study, relatively accurate geolocation estimates were available, but not on a daily basis as there were long periods of time without any estimates due to occupation of relatively deep water. Additional difficulties were presented as a result of conducting light-based analyses on data from high latitudes where relatively long sunrise and sunset events make identifying accurate estimates of day length and local noon particularly challenging (Chittenden et al. 2013).

It is important to acknowledge that relatively large external tags, such as PSATs, have the potential to induce capture/tagging and/or post-tagging effects, thus biasing the results. Specifically, externally attached tags can affect the swimming performance of fishes (e.g., Methling et al. 2011), therefore increasing a fish's susceptibility to predation (e.g., Consgrove et al. 2015). However, because there were no observed relationships among fish size, and mortality, and that some tagged Chinook salmon swam long distances in relatively short periods of time,

PSATs did not appear to have considerably affected the swimming ability of tagged Chinook salmon. The inferred minimal impacts of PSATs on Chinook salmon in this study are similar to the findings for other salmonids (Lacroix et al. 2013; Courtney et al.2016b) and juvenile sandbar sharks *Carcharhinus plumbeus* of similar sizes (Lynch et al. in press). However, future laboratory studies studying the physiological effects of PSAT tagging on Chinook salmon are needed.

Evaluation of project objectives

Overall, we feel that we were successful in achieving our project objectives defined in our research proposal, even though the criterion in objective 1 was not met (capturing and tagging at least one Chinook salmon a day in Dutch Harbor). Accordingly, this objective deserves further discussion to provide context for our conclusion. In 2013 and 2014, we only captured and tagged three Chinook salmon in 17 days of fishing. Because of poor fishing in the 2013 and 2014 seasons, the project Principal Investigators participated in two Japanese research surveys in the Bering Sea during the summers of 2014 and 2015. Participation in the Japanese survey aided project success and allowed the deployment of thirteen tags during the summer (57% of total). In 2015, winter fishing near Dutch Harbor, AK was much more productive, when 31 Chinook salmon >60 cm were captured in just eight days of fishing, and the remaining seven tags were deployed. Given this, if PSATs would not have been deployed during the Japanese cruise, the remaining tags would have been deployed in Dutch Harbor in 2015, and the pre-defined criteria of success for objective 1 would have been met. Longer sampling periods in Dutch Harbor in the winter (November–January) would be of great benefit to the success of future tagging projects.

In contrast to objective 1, objectives 2 and 3 were successfully achieved as rates of capture/tagging survivorship and data retrieval were well above the predefined criteria for success. Comparing PSAT recovery rates (75% in this study) and those from past archival tagging studies in the Bering Sea (3.5% for Chinook salmon, Walker et al. 2005) highlights the utility of fisheries independent tag technology. Given the successful completion of these two project objectives, we consider PSATs to offer a highly feasible method with which to study the oceanic habits of large Chinook salmon.

Conclusion

Information about the diel depth occupancy of Chinook salmon collected in this study may be of particular interest for fisheries managers. For example, during fall and early winter when Chinook salmon have a tendency to be at deeper depths during the daytime and shallower deeps at night, it may be appropriate to operate deep water trawls during the night to reduce bycatch of this species. Furthermore, insights from this study suggest that fisheries population dynamics scientists should revisit the assumptions about ocean mortality of Pacific salmon, and consider the possibility of low survivorship of older age classes of Chinook salmon. Finally, it is important to note that this study had a small sample size of tagged Chinook salmon that were from unknown stocks-of-origin. Therefore, it is highly unlikely that we have provided a comprehensive description of the patterns and variability in the distribution, behavior and thermal environment of Chinook salmon that occupy the Bering Sea. Further investigations with larger sample sizes and geographic scope will be in invaluable to improve our understanding of the oceanic ecology of Chinook salmon, and may inform future management considerations by subsistence users, and biological resource managers.

Table 1. Deployment and end location information for pop-up satellite archival tags attached to 23 Chinook salmon in the Bering Sea (2013–2015).

Fish ID	Capture vessel	FL	Tagging date	Tagging latitude	Tagging longitude	End date	Liberty	Minimum Distance Travelled	% data retrieved	End location latitude	End location longitude
*a*129839	Hokko maru	59	08/02/14	58.50	-180.00	-	-	-	-	-	-
*s*129840	Lucille	79	12/17/14	53.92	-166.62	12/27/14	10	150	100	54.33	-164.49
*a*129841	Hokko maru	72	08/03/14	58.00	-175.00	-	-	-	-	-	-
*a*129842	Hokko maru	62	08/03/14	57.00	-175.00	-	-	-	-	-	-
129843	Lucille	85	12/18/13	53.93	-166.61	04/11/14	114	1470	84	50.68	-145.62
*a*129844	Hokko maru	60	08/05/14	53.00	-175.00	-	-	-	-	-	-
133395	Hokko maru	63	08/03/14	57.00	-175.00	10/20/14	78	541	80	54.78	-167.29
*a*133396	Hokko maru	62	08/03/14	58.00	-175.00	-	-	-	-	-	-
*a*133397	Hokko maru	59	08/05/15	58.00	-175.00	-	-	-	-	-	-
*s*133398	Hokko maru	61	08/03/14	57.00	-175.00	08/13/14	10	245	100	59.03	-176.57
142189	Hokko maru	65	08/05/15	58.00	-175.00	01/01/16	149	252	56	57.85	-170.75
*s*142190	Hokko maru	59	08/05/15	58.00	-175.00	08/12/15	7	151	100	56.72	-174.20
*s*142191	Hokko maru	66	08/07/15	54.00	-175.00	09/09/15	33	389	80	51.96	-170.29
*s*142192	Lucille	68	11/20/15	53.92	-166.61	12/15/15	25	102	5	53.49	-167.18
*u*142193	Hokko maru	68	08/05/15	58.00	-175.00	08/12/15	7	113	99	58.99	-175.39
*m*142194	Lucille	89	11/22/15	53.91	-166.62	12/22/15	30	150	89	55.19	-165.85
*c*142195	Lucille	67	12/18/14	53.92	-166.62	12/18/14	0	1	100	53.93	-166.62
*s*142196	Lucille	70	11/20/15	53.91	-166.61	12/22/15	32	98	93	54.74	-166.11
*u*142197	Lucille	89	11/22/15	53.91	-166.61	01/21/16	60	138	31	54.12	-164.62
*s*142198	Lucille	79	12/02/15	53.91	-166.61	01/22/16	51	530	83	51.65	-172.95
*e*142199	Lucille	79	12/02/15	53.91	-166.61	01/27/16	56	973	91	54.55	-151.83
*c*142200	Lucille	64	11/21/15	53.91	-166.61	11/21/15	0	0	92	53.91	-166.61
148493	Hokko maru	57	08/05/15	58.00	-175.00	08/19/15	14	153	93	57.49	-177.41

a refers to the number of tags which were not accounted for (i.e., missing) on their scheduled pop-up date.
s denotes tags whose data suggested that they were preyed upon by salmon sharks.
m denotes a tag whose data suggested that it was preyed upon by an identified marine mammal.
e denotes a tag whose data suggested that it was preyed upon by an ectothermic fish.
c denotes tags attached to fish which appear to have died due to capture/tagging-induced causes.
u denotes tags whose data suggests an unidentified predation event.

Table 2. Summary statistics of archived depth and temperature readings recorded by pop-up satellite archival tags attached to Chinook salmon.

Fish ID	Mean depth[1] (m)	Depth range (m)	Mean temperature[1] (°C)	Temperature range (°C)	Liberty (days)
*a*129839	-	-	-	-	-
*s*129840	46.2±39.6	0–172	6.15±0.26	5.67–6.63	10
*a*129841	-	-	-	-	-
*a*129842	-	-	-	-	-
129843	127.8±92.6	0–538	5.59±1.21	3.38–8.38	114
*a*129844	-	-	-	-	-
133395	20.6±19.7	0–115	9.56±2.31	3.54–12.8	78
*a*133396	-	-	-	-	-
*a*133397	-	-	-	-	-
*s*133398	4.5±3.7	0–48	11.55±0.63	5.99–12.60	10
142189	45.6±36.6	0–285	4.94±2.76	-0.55–10.57	149
*s*142190	13.8±24.5	0–194	8.92±1.80	3.38–10.57	7
*s*142191	12.4±16.7	0–242	9.9±1.75	4.04–13.53	33
*s*142192*	-	0–328	-	4.37–6.00	25
*u*142193	6.0±13.6	0–124	9.83±1.15	3.04–10.89	7
*m*142194	44.1±28.4	0–172	5.98±0.30	4.53–10.1	30
*c*142195	-	-	-	-	-
*s*142196	74.0±54.7	0–301	5.7±0.44	4.53–6.63	32
*u*142197	22.1±26.2	0–221	5.73±0.48	4.04–6.95	30
*s*142198	71.7±35.6	0–295	5.68±0.38	2.37–6.47	51
*e*142199	43.3±42.0	0–221	5.93±0.39	2.54–6.95	50
*c*142200	-	-	-	-	-
148493	5.3±6.0	0–37.7	10.25±0.45	7.43–10.89	14
Total	50.2±61.3	0–538	6.96±2.73	0.55–13.53	40±42

[1]Depth and temperature are reported as mean±SD.
a refers to the number of tags which were not accounted for (i.e., missing) on their scheduled pop-up date.
s denotes tags whose data suggested that they were preyed upon by salmon sharks.
m denotes tag whose data suggested that it was preyed upon by an identified marine mammal.
e denotes a tag whose data suggested that it was preyed upon by an ectothermic fish.
c denotes tags attached to fish which appear to have died due to capture/tagging-induce causes.
u denotes tags whose data suggests an unidentified predation event.
* Tag # 142192 returned very little data (<5%); therefore, mean depth and temperature occupied are not reported.

Table 3. Description of confirmed predation events of nine tagged Chinook salmon, and occupied depth and thermal characteristics of predators.

Fish ID	Liberty (days)[1]	Predator	Time in predator (days)	Mean depth (m)[2]	Visceral temp. of predator T_s (°C)[2]	Thermal excess T_e (°C)[3]
129840	10	Salmon shark	3.92	22.9±18.8	25.2±1.0	18.8
133398	10	Salmon shark	2.13	118.5±118.9	22.9±1.29	11.5
142190	7	Salmon shark	1.15	0.3±0.3	23.5±0.5	13.4
142191	33	Salmon shark	>1.65	101.3±108.7	21.6±2.1	15.6
142192*	25	Salmon shark	-	-	-	
142194	30	Marine mammal	1.84	1.1±2.8	37.4±0.4	32.4
142196	32	Salmon shark	1.58	56.9±71.8	24.0±1.3	18.9
142198	51	Salmon shark	5.49	72.1±76.0	24.5±1.7	19.2
142199ǂ	50	Ectothermic fish	6–7	125±55.0	-	-

[1] Liberty refers to the time period PSATs were attached to a live fish before it was consumed by a predator.
[2] Occupied depth and stomach temperature (T_s) are represented as mean ± standard deviation.
[3]Thermal excess (T_e) is calculated as the difference between mean stomach temperature (T_s) and mean ambient temperature at predation (T_{a1}) and tag expulsion (T_{a2}).
* Tag # 142192 returned very little data (<5%); therefore, summary characteristics of the predator is not reported.
ǂ Since predation #142199 was by an ectothermic fish and the exact time of predation is not discernable, ambient temperatures before and after predation were not known and thermal excess is not reported. Additionally "Time in predator" is given by a range, based on daily minimum and maximum light readings.

Table 4. Fishing effort, number of PSATs deployed, and number of Chinook salmon >60 cm captured in Dutch Harbor while sampling onboard a sport fishing vessel.

Year	Fishing effort (days)	PSATs deployed (n)	Kings caught > 60 cm (n)
2013	8	1	1
2014	9	2	3
2015	8	7	31
Total	25	10	35

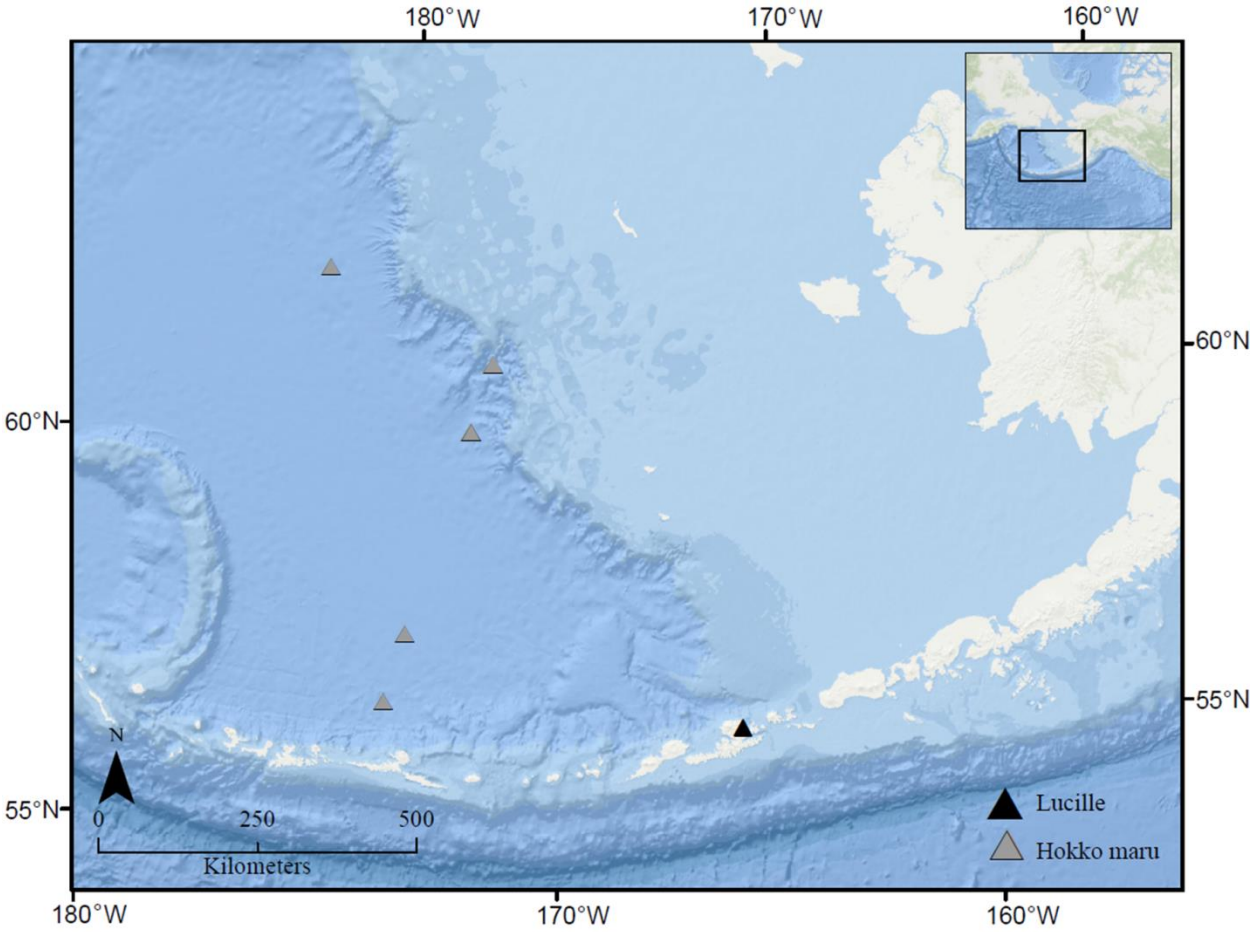

Figure 1. Tagging locations of pop-up satellite archival tagged Chinook salmon, by tagging vessel. Chinook salmon released aboard the F/V Lucille were captured by hook-and-line in mid-November to December 2013–2015. Fish released on the R/V Hokko maru were captured by hook-and-line and by midwater trawl, in late July/early August 2014–2015.

Figure 2. Pop-up satellite archival tagged Chinook salmon in custom fabricated tagging cradle and flowing sea-water (top panel) and close up image of the tagging harness used in this study (bottom panel; taken from Courtney et al. 2016b).

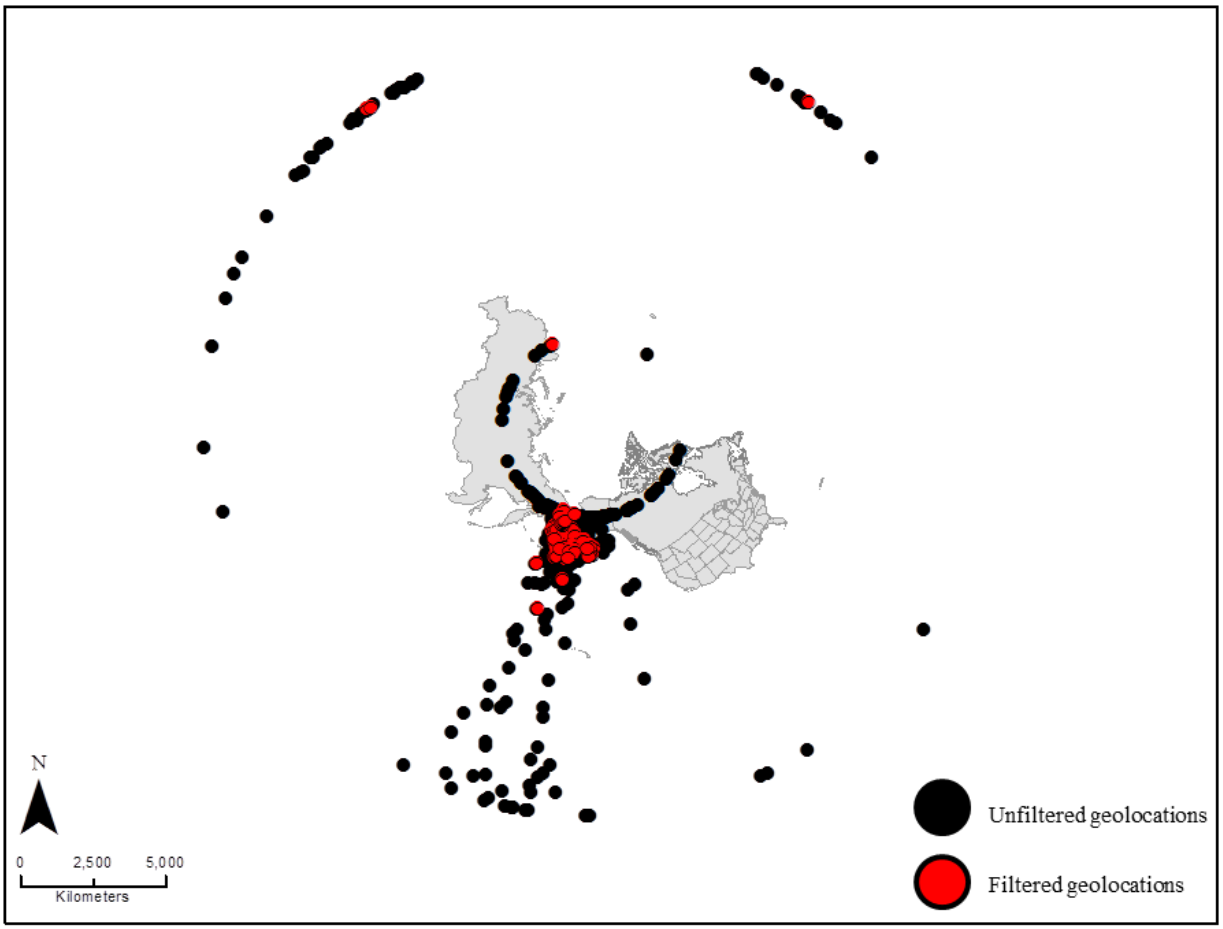

Figure 3. Map showing all daily geolocation estimates from 17 PSATs attached to Chinook salmon that reported to satellites. Daily geolocation estimates were produced by a proprietary algorithm written by the tag manufacturer and were based on sunrise and sunset events calculated by the tags. Filtered daily geolocation estimates are a subset all geolocation estimates (i.e., 'unfiltered') and contain locations for which sunrise and sunset times were determined by PSATs at a depth <10 meters, and were not within 10 days of autumn or spring equinoxes.

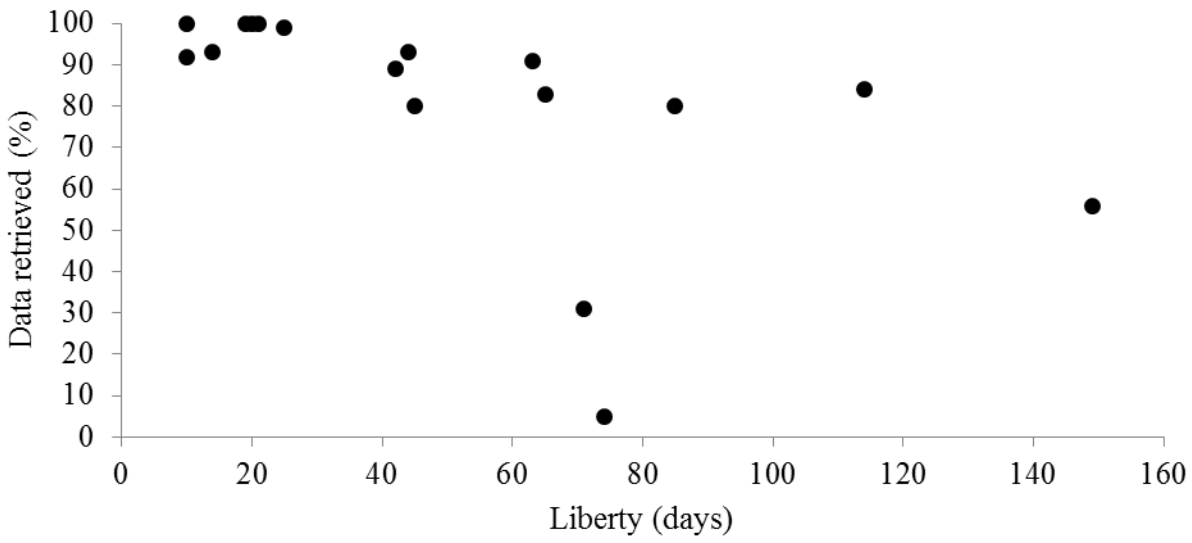

Figure 4. Percentage of retrieved data from individual pop-up satellite archival tags attached to Chinook salmon compared to time at liberty (days) for each fish (n =17) whose tags reported satellites.

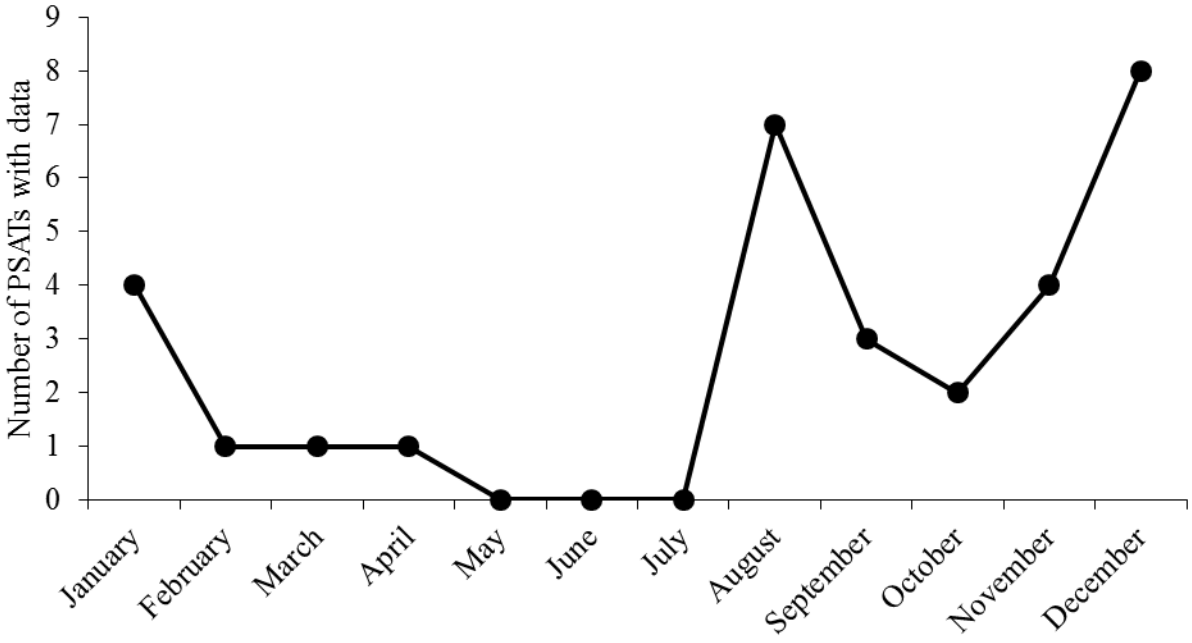

Figure 5. Monthly number of pop-up satellite archival tags that provided data about Chinook salmon in the ocean.

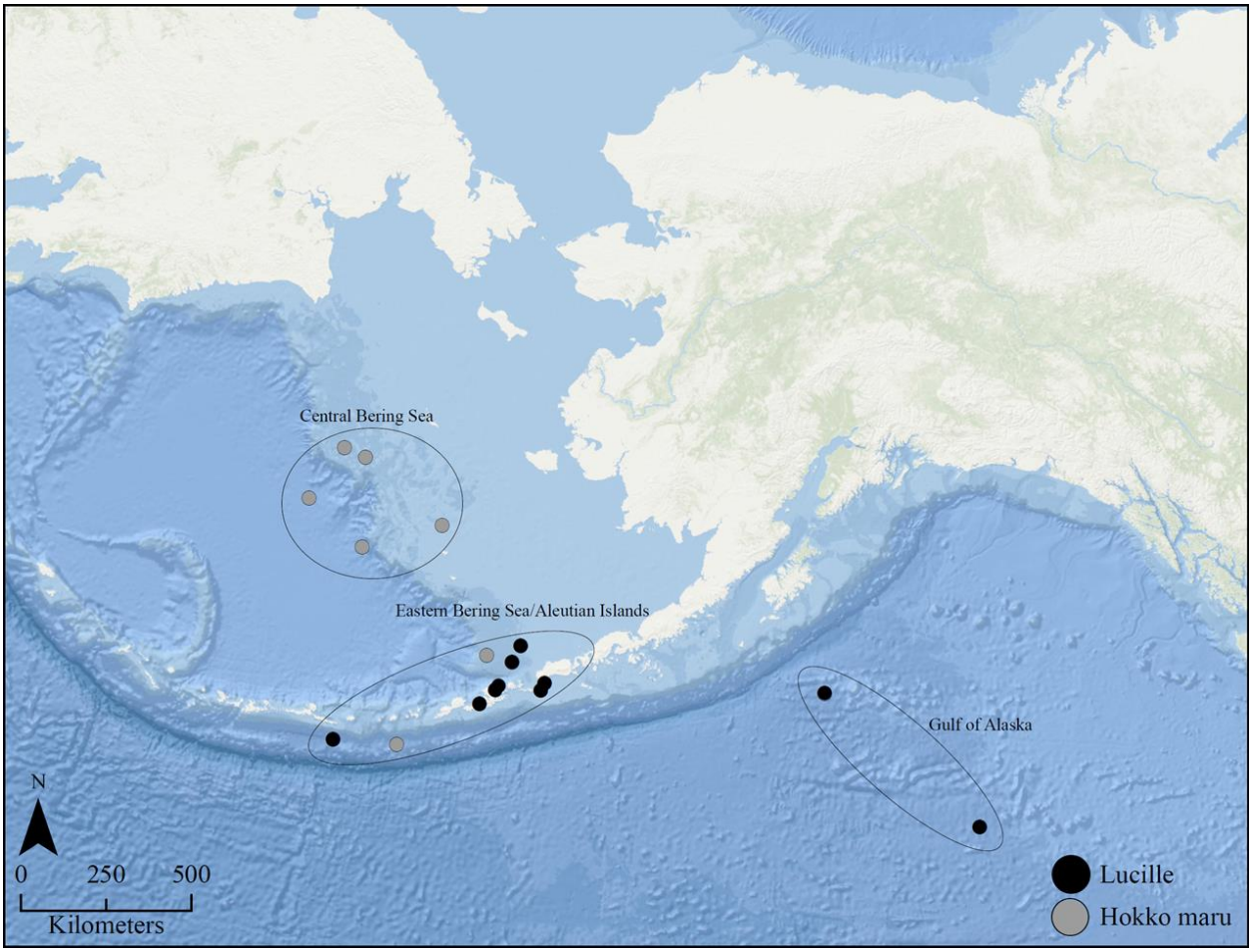

Figure 6. End locations of pop-up satellite archival tagged Chinook salmon, by capture vessel. Chinook salmon released aboard the F/V Lucille were captured by hook-and-line in mid-November to December 2013–2015. Fish released on the R/V Hokko maru were captured by hook-and-line and by midwater trawl in late July/early August 2014–2015. Aggregations of end locations are defined by prominent geographic regions for interpretation purposes.

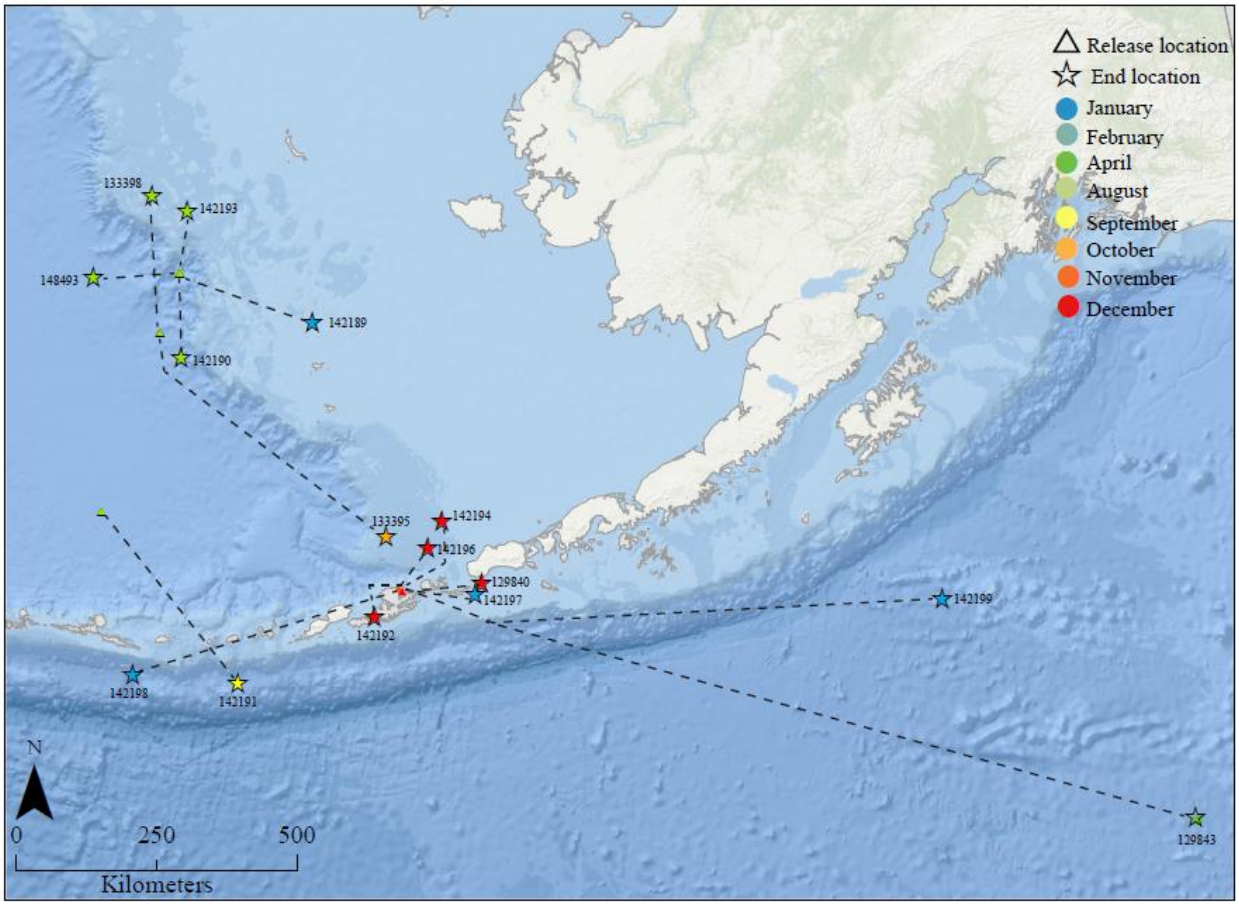

Figure 7. Tagging (triangles) and end locations (stars) of Chinook salmon, color coded by month of the year. Dashed lines denote straight-line path between tagging and end locations. Tag identification numbers are provided by each tag's end location.

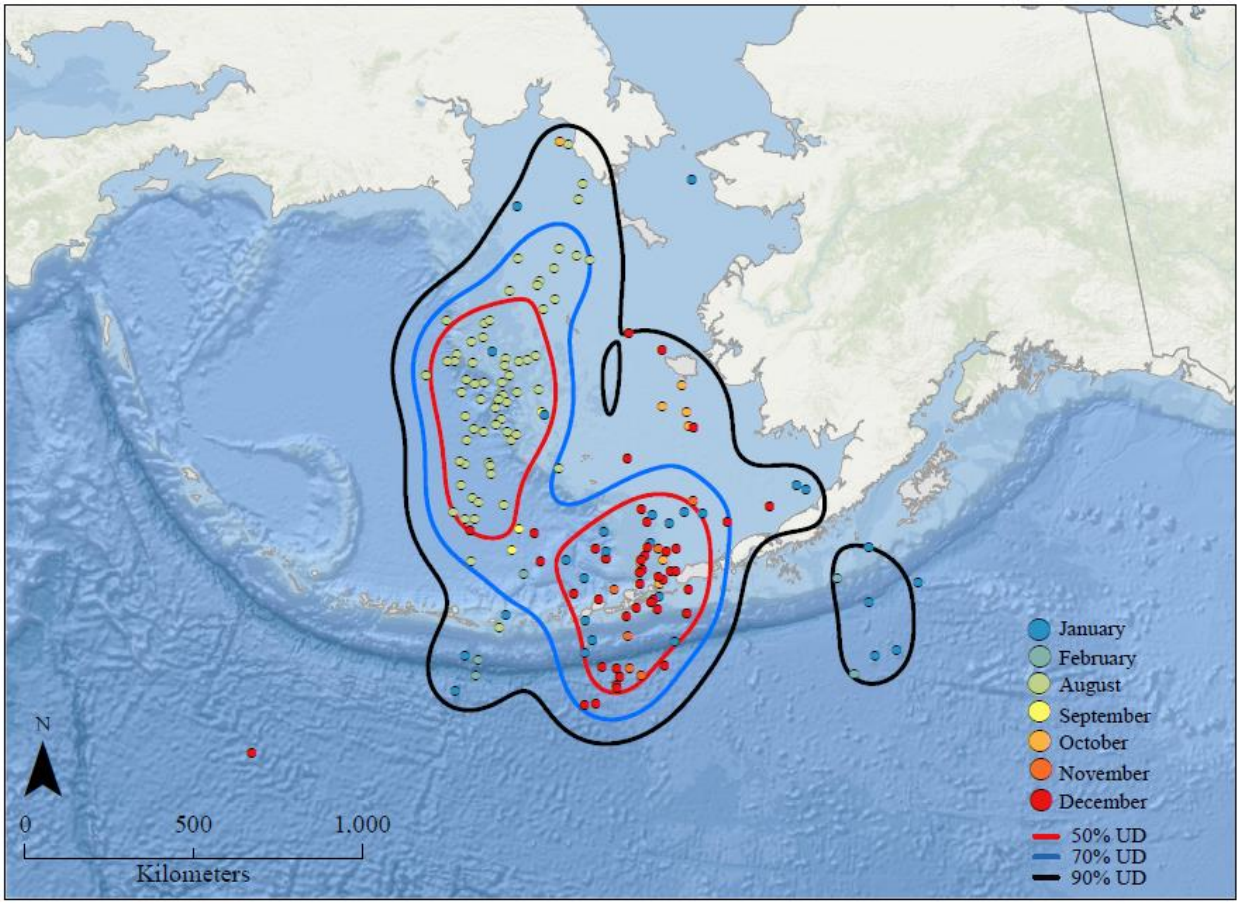

Figure 8. Filtered daily geolocation estimates (color coded by month) and utilization distributions (UD) of all Chinook salmon tagged with pop-up satellite archival tags.

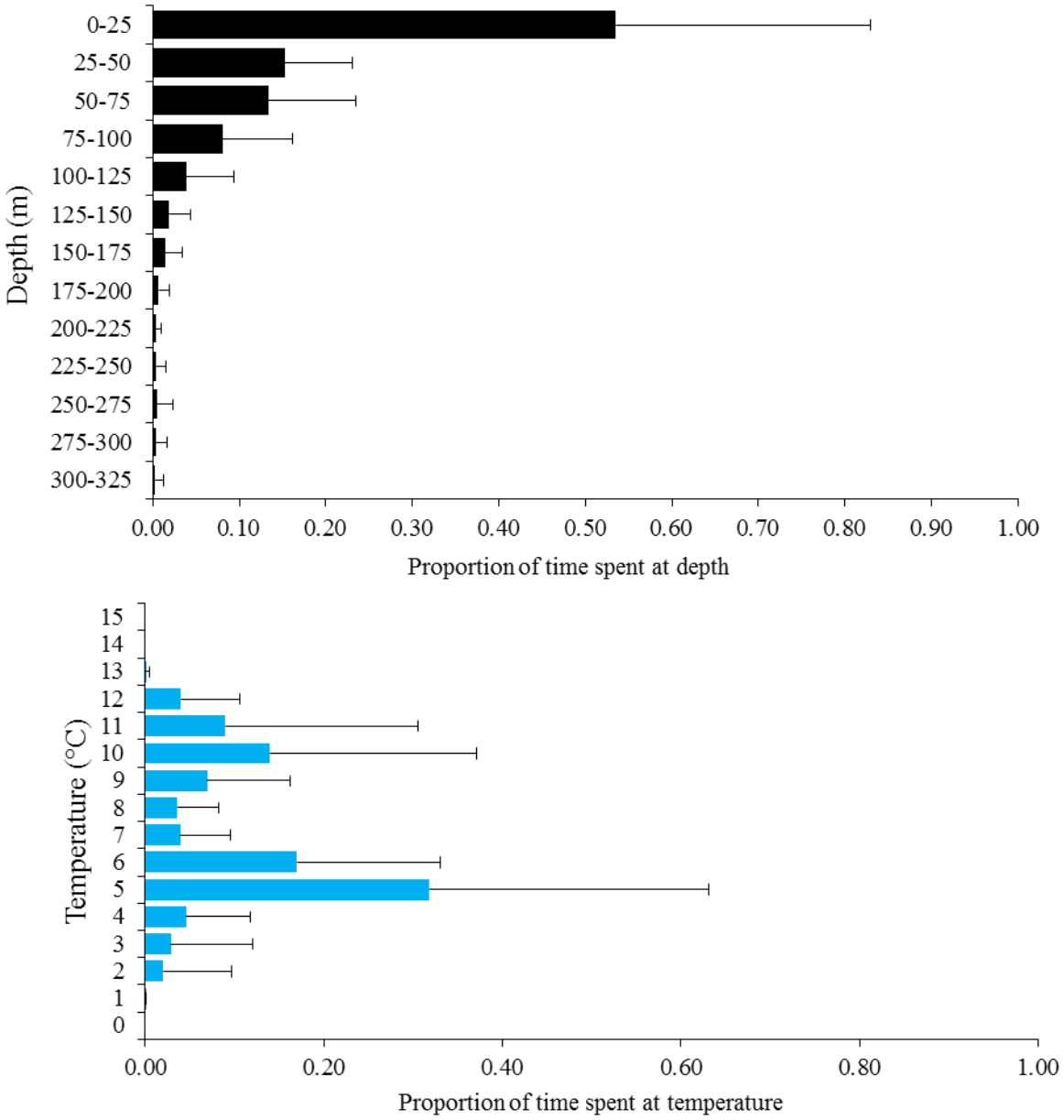

Figure 9. Mean proportion (± SD) of time spent at depths (top) and temperatures (bottom) by all Chinook salmon.

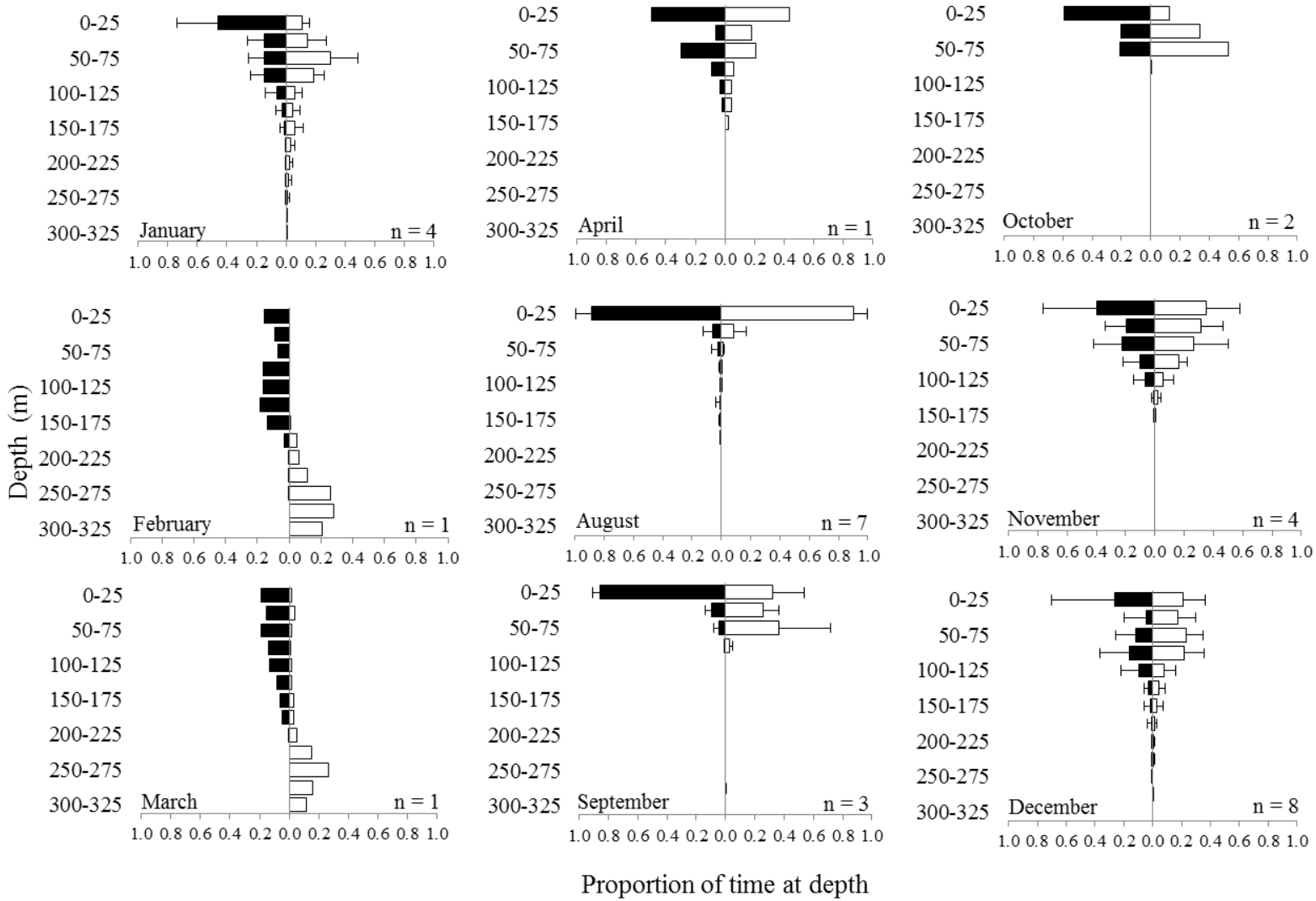

Figure 10. Monthly mean proportion (±SD) of time spent at depth by all Chinook salmon. Black and white bars denote periods of night and day respectively. * denotes months in which significant differences ($p < 0.05$) in monthly mean depth occupation between night and day were found. Number of tags providing data for each monthly calculation is indicated.

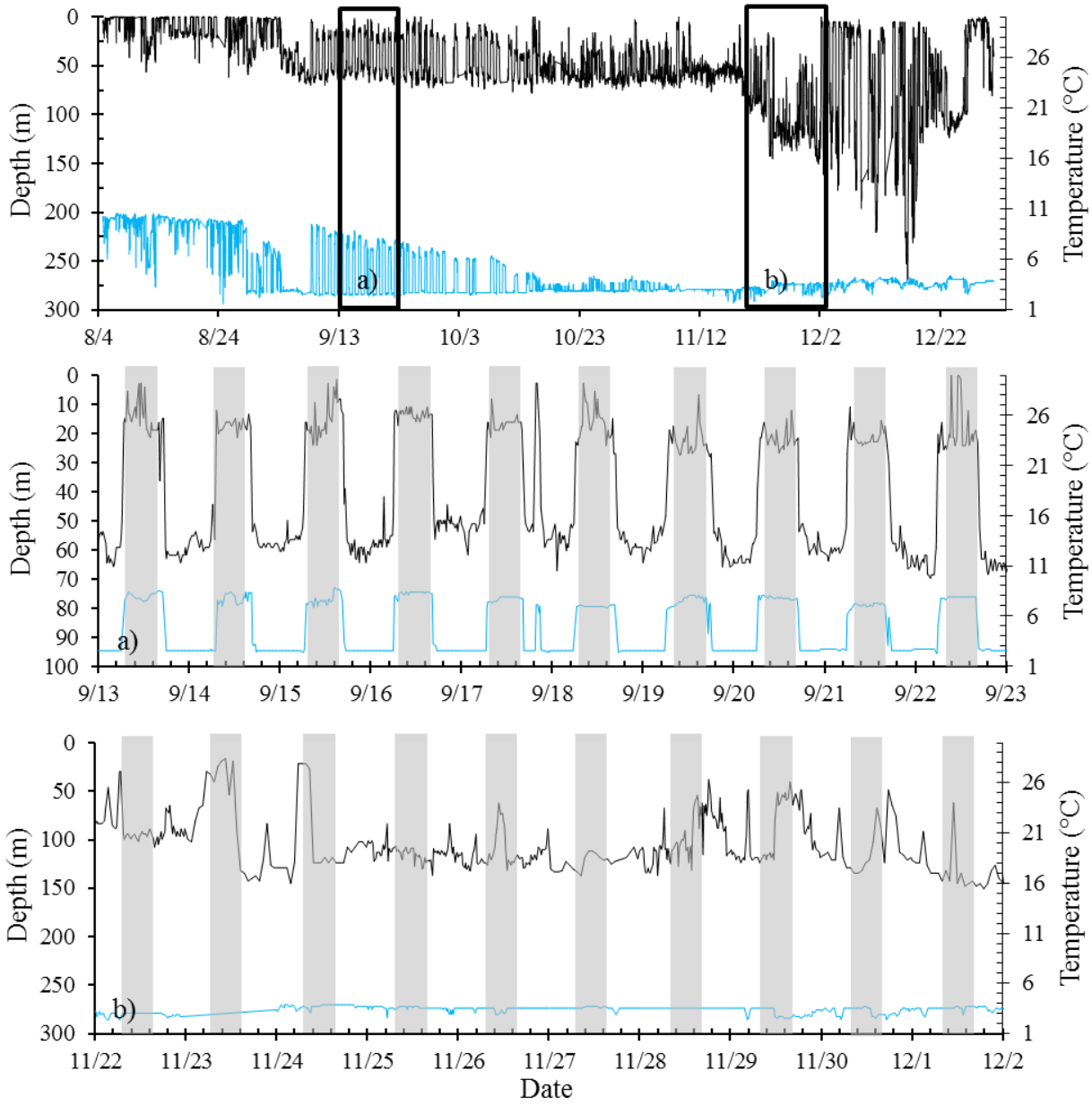

Figure 11. Example of diel and non-diel diving behavior of a tagged Chinook salmon (#142189) that resided in the central Bering Sea. Zoomed insets denoted by rectangles in the upper panel are time periods of a) diel and b) non-diel diving behaviors. Depth (black line) and temperature (blue line) values were recorded every 15 minutes. Gray bars denote hours of darkness.

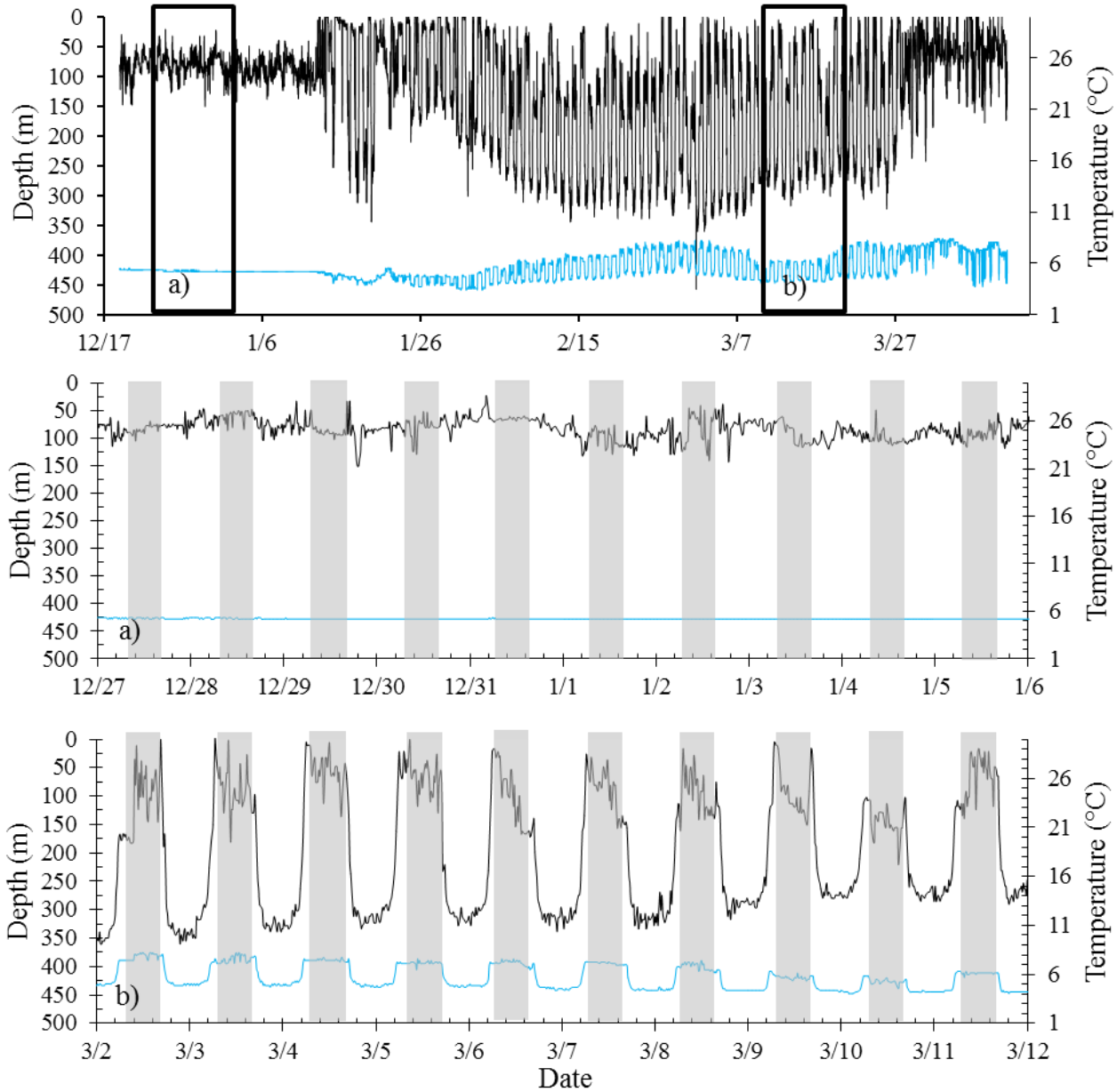

Figure 12. Example of diel and non-diel diving behavior of a tagged Chinook salmon (#129843) that was tagged near Dutch Harbor, AK and whose end location was in the Gulf of Alaska. Zoomed insets denoted by rectangles in the upper panel are time periods of a) diel and b) non-diel diving behaviors. Depth (black line) and temperature (blue line) values were recorded every 15 minutes. Gray bars denote hours of darkness.

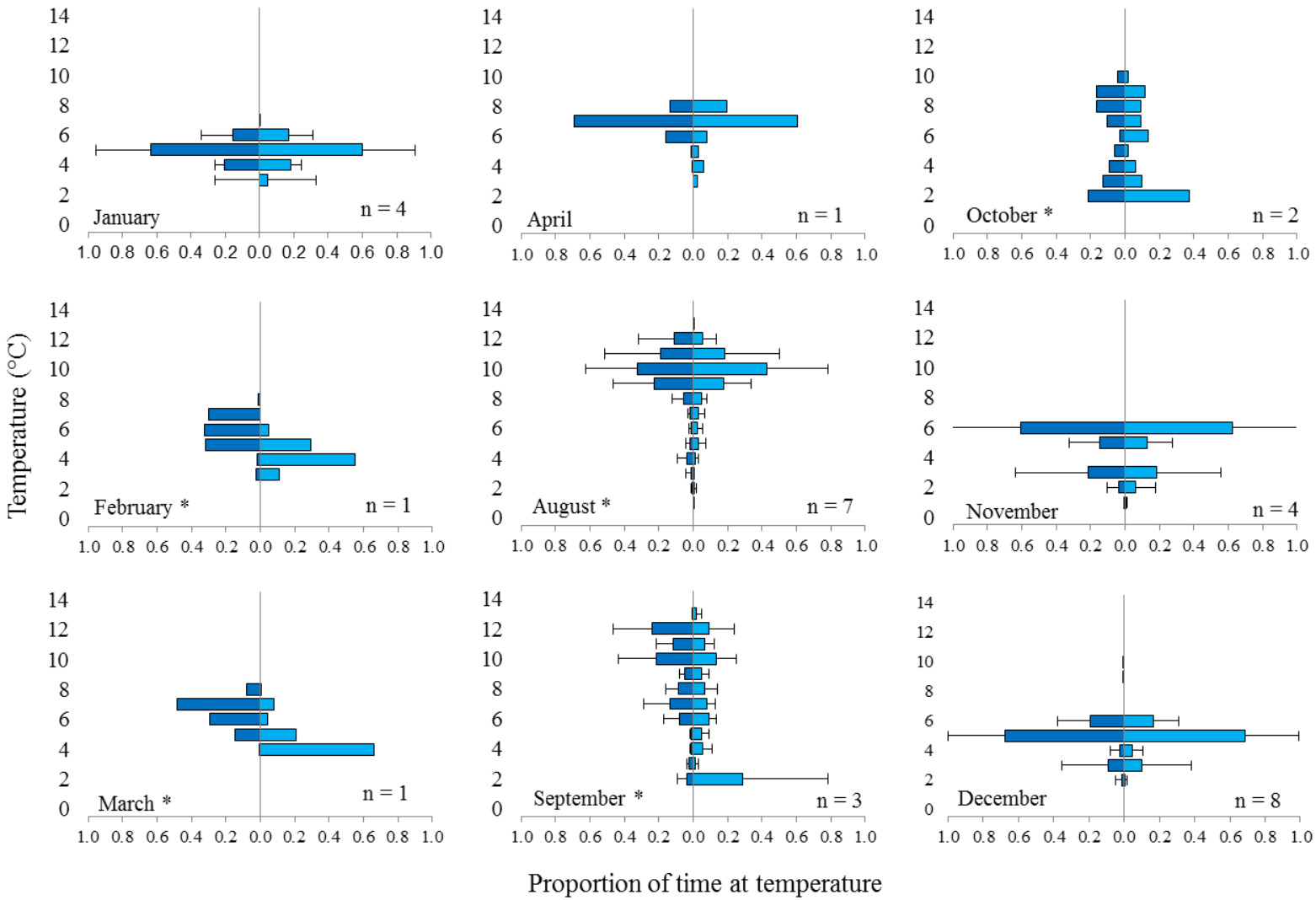

Figure 13. Monthly mean proportion (± SD) of time spent at temperatures by all Chinook salmon. Dark blue and light blue bars denote periods of night and day respectively. * denotes months in which significant differences ($p < 0.05$) in monthly mean temperatures between night and day were found. Number of tags providing data for each monthly calculation is indicated.

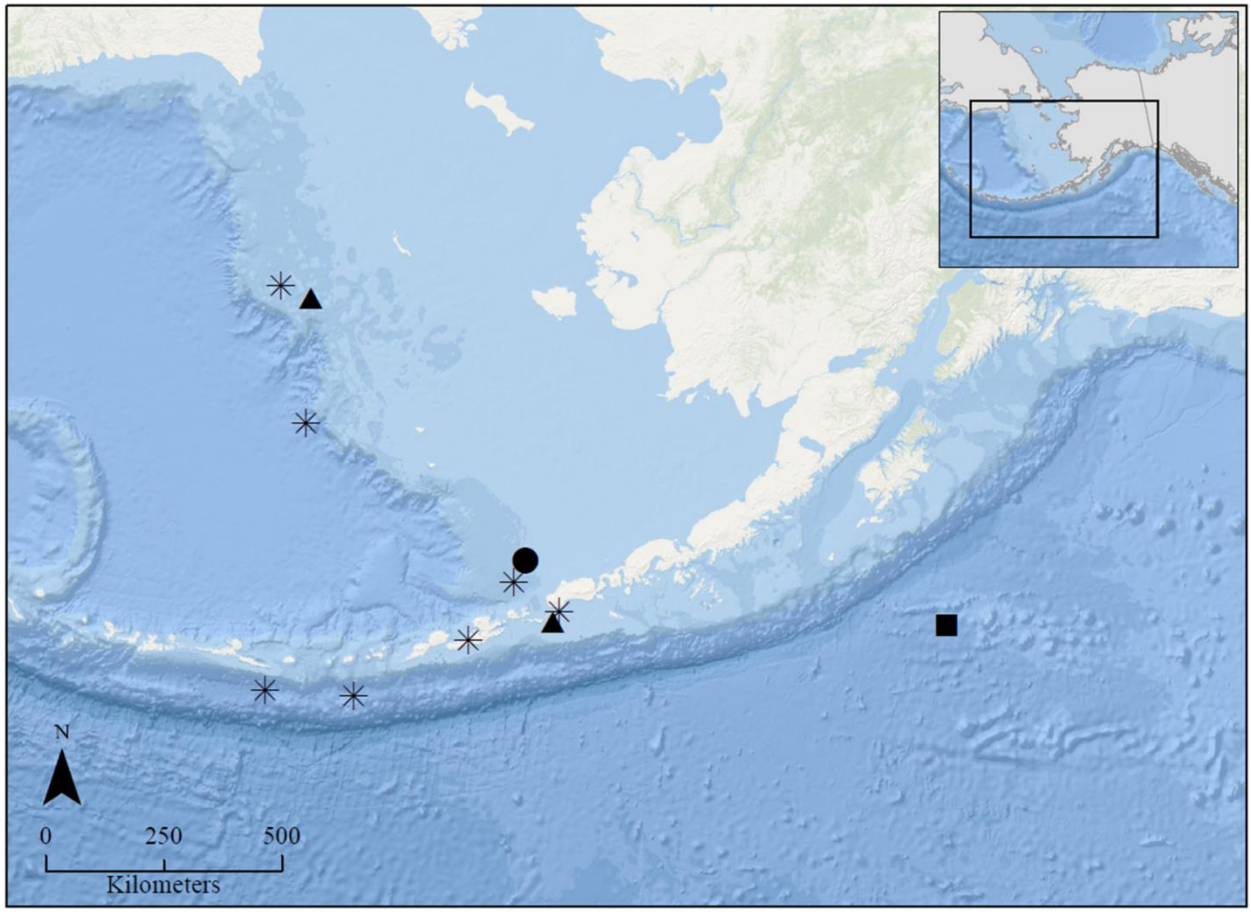

Figure 14. End locations of Chinook salmon whose PSATs provided evidence that they were preyed upon by salmon sharks (asterisks), a marine mammal (circle), an ectothermic fish (square), and unconfirmed predators (triangles).

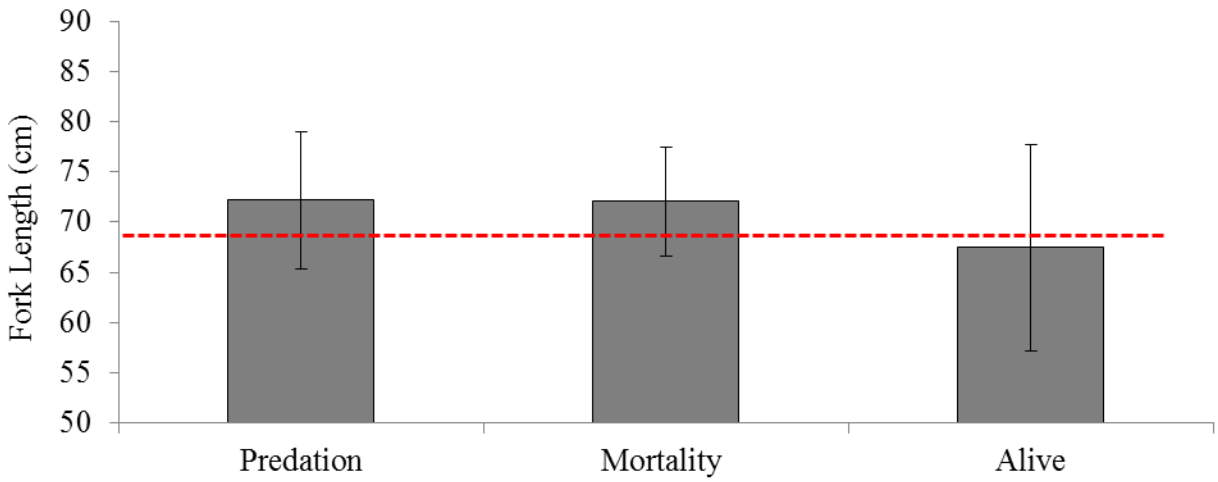

Figure 15. Means and 95% confidence intervals of length of tagged Chinook salmon that were classified as dead or alive on their pop-up date. “Predation” denotes tags whose data suggested confirmed predation. “Mortality” denotes tags whose data suggested that they either experienced confirmed predation, unconfirmed predation, or tag/capture-induced mortality. “Alive” denotes tagged fish that were alive on their pop-up dates. The dashed (red) horizontal line is the mean fork length of all tagged Chinook salmon.

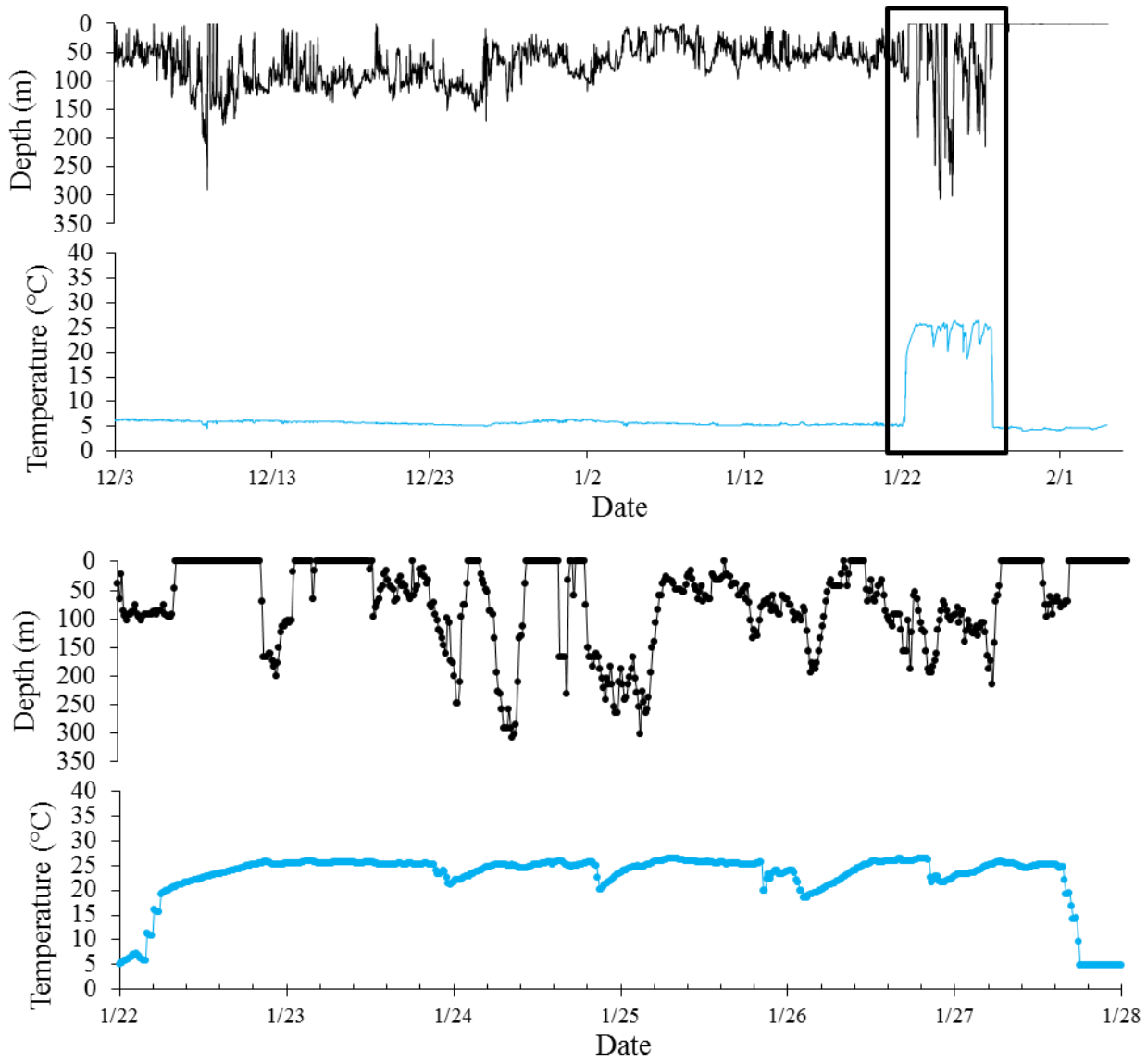

Figure 16. Example of salmon shark predation on a Chinook salmon in the Bering Sea. The black rectangle (upper panel) denotes the extent of the bottom panel. Depth (black line) and temperature (blue line) values were recorded every 15 minutes.

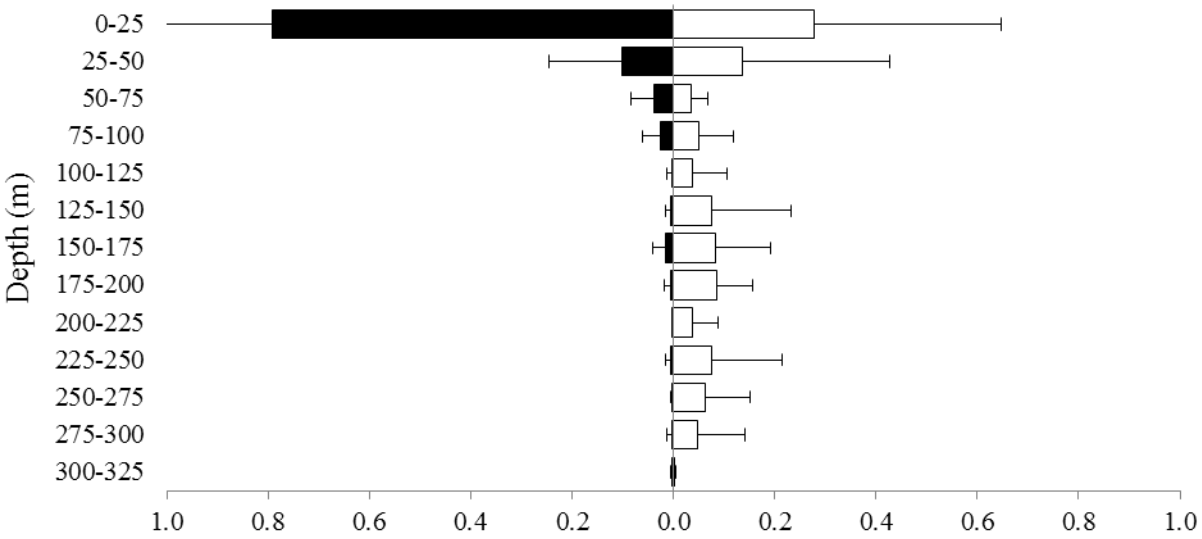

Figure 17. Mean proportion (± SD) of time spent at depths for all salmon sharks. Black and white bars denote periods of night and day respectively.

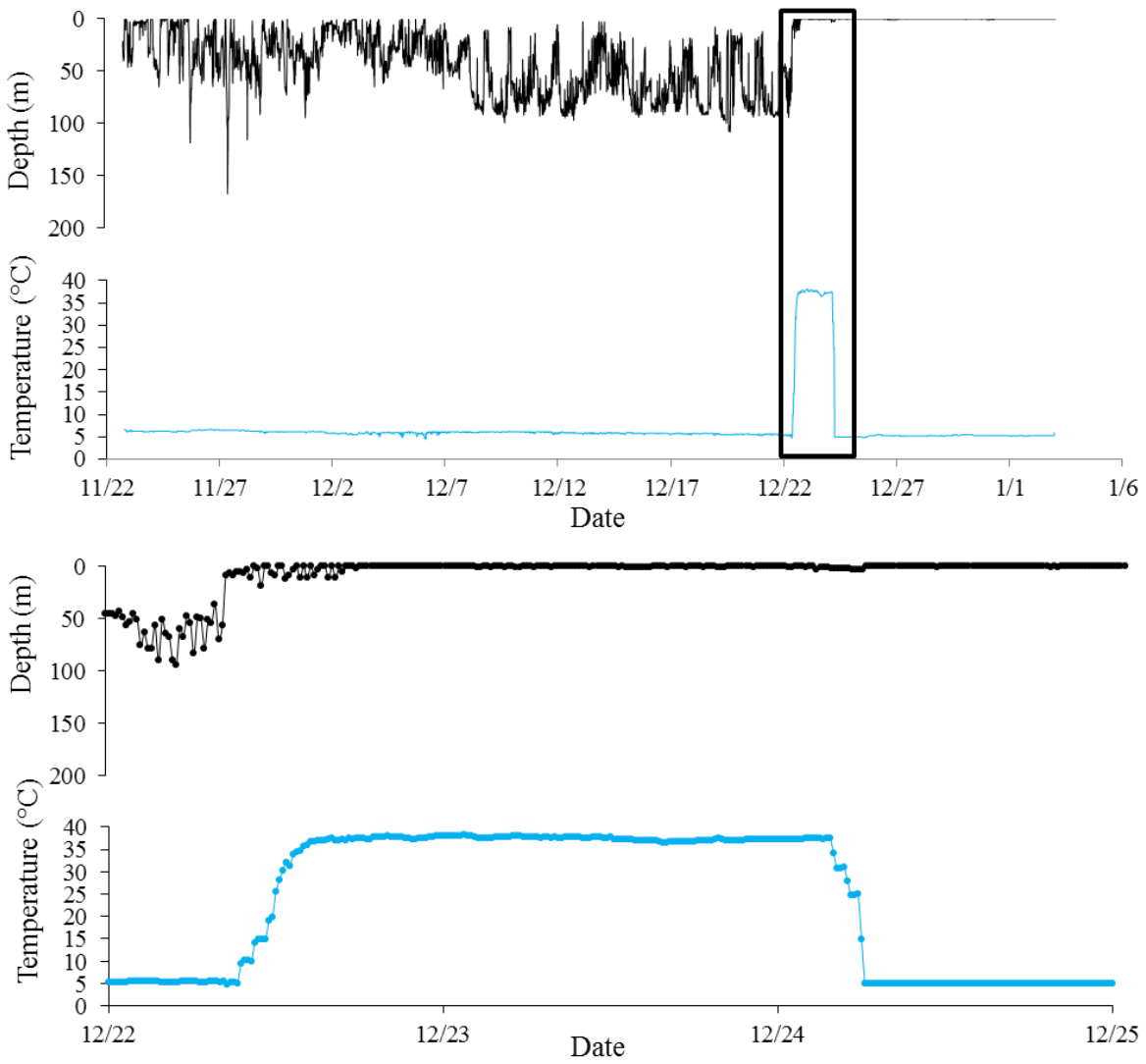

Figure 18. Example of Chinook salmon predation by a marine mammal. The black rectangle (upper panel) denotes the extent of the bottom panel. Depth (black line) and temperature (blue line) values were recorded every 15 minutes.

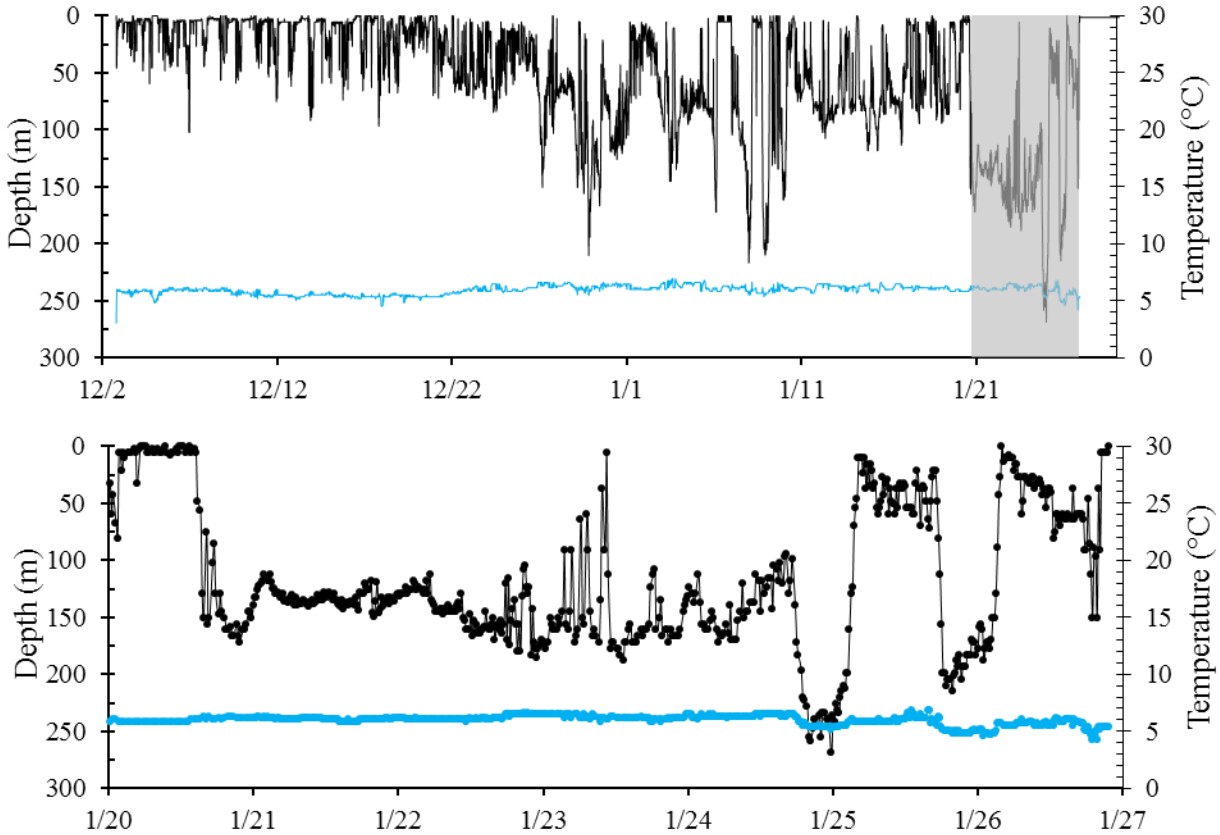

Figure 19. Example of a predation event by an ectothermic fish. Gray box (top panel) denotes a time period of complete darkness, and the extent of the bottom panel. Depth (black line) and temperature (blue line) values were recorded every 15 minutes.

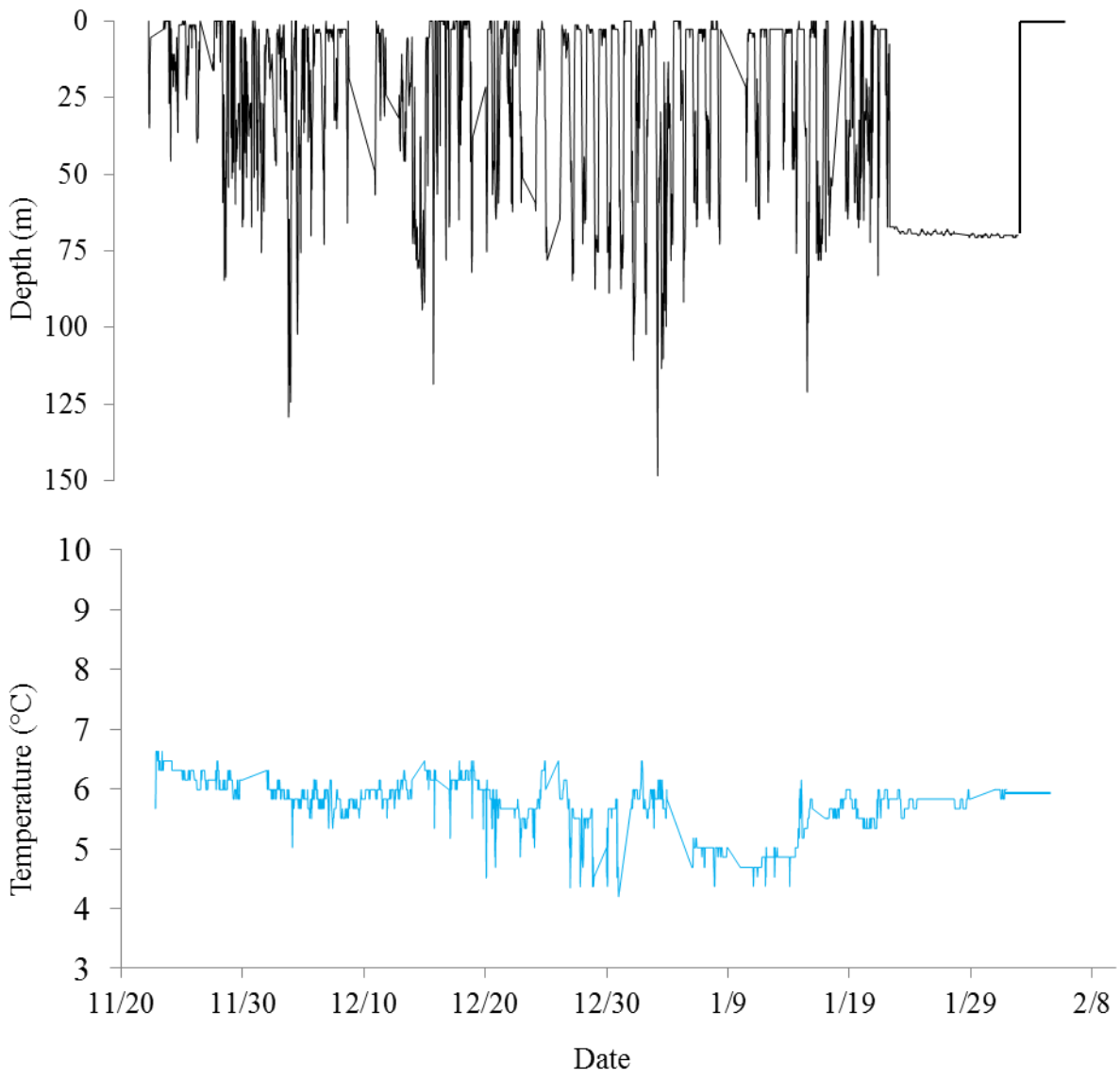

Figure 20. Example of an unconfirmed predation event on a Chinook salmon for which the identity of the predator is unknown. Depth (black line) and temperature (blue line) values were recorded every 15 minutes.

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Seitz, A. C., M. B. Courtney, M. D. Evans, and J. Murphy. 2016. Life and death of big Chinook salmon in the Bering Sea. University of Alaska Fairbanks Fisheries Division Seminar Series, April 2016.

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Project Data

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Press Release

While Pacific salmon are widely distributed in offshore waters of the North Pacific Ocean, and of great economical and subsistence importance, little is known about their oceanic ecology. To address this knowledge gap, we tested the efficacy of pop-up satellite archival tags (PSATs) to provide insights into the oceanic movements, survivorship, behavior and thermal environment of Chinook salmon in the Bering Sea. Tagged Chinook salmon ranged widely between the north-central Bering Sea, the central Aleutian Islands, and the central Gulf of Alaska. While at liberty, Chinook salmon spent the majority of their time in the first 25 m of the water column (0–538 m range), occupying a thermal environment of mostly 5–11°C. PSATs provided evidence of predation on tagged Chinook salmon by salmon sharks, marine mammals, ectothermic fish, and unidentified predators, over a wide range of the Bering Sea and Gulf of Alaska. High mortality estimates in this study suggest low marine survivorship of large immature and maturing Chinook salmon. Further investigations on marine survivorship will be valuable for improving our understanding of the oceanic ecology of Chinook salmon, and may inform future management considerations by subsistence users and biological resource managers.